Diversity and resource choice of flower-visiting insects in relation to pollen nutritional quality and land use

Diversität und Ressourcennutzung Blüten besuchender Insekten in Abhängigkeit von Pollenqualität und Landnutzung

Vom Fachbereich Biologie der Technischen Universität Darmstadt

zur

Erlangung des akademischen Grades

eines Doctor rerum naturalium

genehmigte

Dissertation von

Dipl. Biologin Christiane Natalie Weiner

aus Köln

Berichterstatter (1. Referent): Prof. Dr. Nico Blüthgen

Mitberichterstatter (2. Referent): Prof. Dr. Andreas Jürgens

Tag der Einreichung: 26.02.2016
Tag der mündlichen Prüfung: 29.04.2016
Darmstadt 2016
D17

Ehrenwörtliche Erklärung

Ich erkläre hiermit ehrenwörtlich, dass ich die vorliegende Arbeit entsprechend den Regeln guter wissenschaftlicher Praxis selbständig und ohne unzulässige Hilfe Dritter angefertigt habe. Sämtliche aus fremden Quellen direkt oder indirekt übernommene Gedanken sowie sämtliche von Anderen direkt oder indirekt übernommene Daten, Techniken und Materialien sind als solche kenntlich gemacht. Die Arbeit wurde bisher keiner anderen Hochschule zu Prüfungszwecken eingereicht.

Osterholz-Scharmbeck, den 24.02.2016

My doctoral thesis is based on the following manuscripts:

Weiner, C.N., Werner, M., Linsenmair, K.-E., Blüthgen, N. (2011): **Land-use intensity in grasslands: changes in biodiversity, species composition and specialization in flower-visitor networks.** Basic and Applied Ecology 12 (4), 292-299.

Weiner, C.N., Werner, M., Linsenmair, K.-E., Blüthgen, N. (2014): **Land-use impacts on plant-pollinator networks: interaction strength and specialization predict pollinator declines.** Ecology 95, 466–474.

Weiner, C.N., Werner, M , Blüthgen, N. (in prep.): **Land-use intensification triggers diversity loss in pollination networks: Regional distinctions between three different German bioregions**

Weiner, C.N., Hilpert, A., Werner, M., Linsenmair, K.-E., Blüthgen, N. (2010): **Pollen amino acids and flower specialization in solitary bees.** Apidologie 41 (4), 476-487.

Pantoum on Nature's Patience

(by Mark R Slaughter)

Surviving all to seize the hour;
A firm reward: a solitary flower.
With pinch of time to propagate -
Of seed and chance, it must await.

A firm reward: a solitary flower,
But motionless, the dainty tower.
Of seed and chance, it must await
And not by dreams or wishing fate.

But motionless, the dainty tower -
Completion lies in gusty power,
And not by dreams or wishing fate.
Unmindful patience; whither date?

[…]

Pulsatilla vulgaris © Christiane N. Weiner

Inhaltsverzeichnis

Summary

Recent declines in honey bee colonies as well as in the diversity and abundance of native pollinators generated widespread concern about the future of pollination and set off a discussion about a general “pollination crisis”. Partly, this is due to the functional importance of this ecosystem service not only for plant reproduction but above all for crop production and thus human welfare. Consequently, the matter gained particular attention in current research and a rising number of studies focus on the stability of plant-pollinator interactions in relation to biodiversity and ecosystem change.

My dissertation focuses on the mutualistic interactions between flowering plants and flower-visiting insects and their interactive response to land-use intensity as well as resource choice of flower-visitors in relation to pollen quality. The innovative approach of my project is to use quantitative interaction networks to provide knowledge on how species respond to land use and how their responses may influence their interaction partners. We show that information from ecological networks may help to predict natural community responses to disturbance and possible secondary extinctions in systems that undergo agricultural intensification, if the identity of each species’ partners and relative interaction strengths are considered. This project presents large-scale investigations on the characteristics and fragility of multi-species networks in real landscapes. During two seasons we recorded the diversity, species composition and specialization of plant-pollinator networks along a gradient of increasing land-use intensity. The study was conducted within the framework of the Biodiversity Exploratories, which are located in the Schorfheide-Chorin (NE Germany), Hainich-Dün (Central Germany) and Schwäbische Alb (SW Germany) regions. Each Exploratory contains 50 experimental grassland plots which comprise near natural, protected sites as well as intensively fertilized, mown or grazed meadows and pastures.

Comparing meadows of high and low land-use intensities we found that species richness of plants, bees and butterflies was significantly higher on low intensity meadows. However, in terms of Shannon diversity and abundance only butterflies

responded negatively to land-use intensification (Chapter 2). Nevertheless, the analysis of plant and flower-visitor composition revealed crucial differences between grassland types with species overlaps of just 43 % in plants and 42 % in insects. This pointed to the fact that investigation of biodiversity and abundance alone may not detect biotic homogenization e.g. a loss in functional diversity. Moreover, resource impoverishment had stronger effects on the land-use response of highly specialized flower-visitor groups than on little or unspecialized ones.

We examined if mutual specialization could explain the accelerating parallel declines observed in plants and pollinators. Focusing on their stability, we analyzed 162 plant-pollinator networks from 119 meadows and pastures managed at different intensities. The fate of a flower visitor was predicted by the land-use response of its associated plant species and vice versa. Furthermore, we detected a disproportional impact of land-use intensification on the abundance of more specialized pollinator species (Chapter 3). Land-use intensification seems to set off losses in flower diversity, which leads to resource-mediated declines in pollinator species. While the mean land-use response of the pollinators visiting a plant species also influenced its abundance, this effect was weaker. Network analyses provide a valuable tool for characterizing mutualisms in a community context and may be used to predict community responses to disturbance and possible consequences of species loss.

To further illuminate which land-use practices most fundamentally influence plant-pollinator associations, we analyzed the isolated effects of fertilization, mowing and grazing intensity on plant – flower-visitor networks (Chapter 4). I found that these three components of land use strongly differed in their effects on the species richness and composition of flower-visitor networks. While increases of fertilization and mowing intensity in two out of three bioregions were accompanied by a decrease in plant species richness, concerning pollinator species richness, abundance and composition trends were even more conflictive between taxonomically different pollinator groups and between regions. Thus, the results showed that it is not possible to readily transfer results and management recommendations from one region to another. Yet, I found that across all three regions pollinator fate was determined by the average land-use response of the plant species they visited and vice versa (Chapter 4). Moreover, in pollinators –

but not in plants – specialized species were disproportionately affected by land-use intensification.

Specialized pollinators such as oligolectic bees (bees that collect pollen only from one plant family or even just from one single species) are often expected to be more prone to disturbance and thus more vulnerable to ecosystem change. This is recognized as the cost of specialization and was reinforced by my results (Chapter 3 and 4). On the other hand it has frequently been proposed that benefits from resource specialization may outweigh the costs. In pollinators, benefits of specialization so far were presumed to result from higher foraging efficiency. Among the various adaptations is assumed specialization on very nutrient-rich pollen.
We therefore analyzed hand-collected pollen from 142 plant species for its quantitative and qualitative amino acid composition. The composition of amino acids varied strongly among plant species, but taxonomically related species had similar compositions. Surprisingly, the concentration of free- and protein-bound amino acids – also of the essential ones – was significantly lower in pollen sources used by oligolectic bees than in other pollen sources (Chapter 5). Moreover, pollen sources of oligoleges deviated more strongly from the ideal composition of essential amino acids as determined for honey bees than plants not hosting oligolectic bees. This leads to the assumption that competitive avoidance or in other words an advantage in terms of the available pollen quantity might have led to oligolectic bees being specialized on pollen that is deficient in amino acids. This hypothesis still needs to be tested in detail.

Several of the results presented in this thesis shed new light on patterns and processes within plant-pollinator interactions. We found that – contrary to the prevailing contemporary opinion – plant-pollinator networks are highly specialized systems in which the diversity of plants and pollinators is strongly related to each other.

Zusammenfassung

Das Bienen-Sterben in den USA und Europa sowie der Rückgang der Diversität und Abundanz heimischer Blütenbesucher haben weltweit Sorge um die Zukunft der Pollination geschürt – und eine hitzige Diskussion über eine allgemeine „Pollinationskrise“ losgetreten. Dies ist zum Teil der funktionellen Bedeutung der Pollination als Ökosystem-Dienstleistung im Allgemeinen geschuldet. Eine erfolgreiche Pollination ist nicht nur für die Reproduktion von Blütenpflanzen, sondern auch für die Nahrungsmittelproduktion – und somit auch für den Wohlstand des Menschen – von größter Bedeutung. Dementsprechend legt die aktuelle Forschung ein besonderes Augenmerk auf dieses Thema und eine stetig wachsende Anzahl an Studien beschäftigt sich in Verbindung mit Biodiversitätsverlust und Ökosystemwandel mit der Stabilität der Interaktionen zwischen Pflanzen und Bestäubern.

Meine Dissertation konzentriert sich auf die mutualistischen Interaktionen zwischen Blütenpflanzen und Blüten besuchenden Insekten und ihre interaktive Reaktion auf die Intensivierung der Landnutzung sowie auf die Ressourcenwahl Blüten besuchender Insekten in Abhängigkeit von Pollenqualität. Der neuartige Ansatz des hier präsentierten Projekts ist es, quantitative Interaktionsnetzwerke zu nutzen, um aufzuzeigen, wie eine Art auf Landnutzung reagiert und wie ihre Reaktion ihre Interaktionspartner beeinflusst. Betrachtet man die Identität der Partner einer Art sowie die Interaktionsstärken, lässt sich darauf schließen, wie natürliche Lebensgemeinschaften auf Störungen reagieren und welche sekundären Aussterberisiken für Arten in Ökosystemen, die landwirtschaftlicher Intensivierung unterliegen, möglicherweise resultieren. Mein Projekt ist eine der ersten breit angelegten Untersuchungen über die Charakteristiken und die Fragilität der Beziehungen zwischen verschiedenen Spezies in real existierenden Ökosystemen, die einer sich intensivierenden Flächennutzung unterliegen. Über zwei Vegetationsperioden hinweg haben wir verschiedene Charakteristika der Beziehungen von Pflanzen und den sie besuchenden Insekten entlang eines Landnutzungsgradienten im Grünland untersucht. Die Studie wurde innerhalb des Großprojektes der Biodiversitäts-Exploratorien durchgeführt, die jeweils 50 experimentelle Grünlandflächen in Nordost-,

Zentral- und Südwestdeutschland (Schorfheide-Chorin, Hainich-Dün, Schwäbische Alb) umfassen. Diese Grünlandflächen repräsentieren Nutzungstypen, die von naturnahen, geschützten Flächen bis hin zu intensiv gedüngten, häufig gemähten oder intensiv beweideten Flächen reichen.

Ein Vergleich zwischen intensiv und extensiv genutzten Wiesen ergab, dass die Abundanz von Pflanzen, Bienen und Schmetterlingen auf extensiv genutzten Wiesen signifikant höher war als auf intensiv genutzten. Bezüglich der Diversität ließ sich ein negativer Einfluss höherer Landnutzungsintensität dagegen nur für Schmetterlinge nachweisen (Kapitel 2). Dennoch zeigte eine Analyse der Artenzusammensetzung von Pflanzen und Blütenbesuchern erhebliche Unterschiede zwischen den Nutzungstypen auf. Die Artüberschneidung betrug lediglich 43 % bei Pflanzen und 42 % bei Blütenbesuchern. Ein klarer Hinweis darauf, dass die Untersuchung von Biodiversität und Abundanz alleine nicht ausreicht, um eine biotische Homogenisierung und damit einen Schwund der funktionalen Diversität nachzuweisen. Außerdem hatte die mit der Landnutzungsintensivierung einhergehende Ressourcen-Verknappung stärkere Auswirkungen auf die Reaktion spezialisierter Pollinatoren-Gruppen, als auf die Reaktion solcher, die als nicht oder kaum spezialisiert angesehen werden können.

Daher wollten wir herausfinden, ob sich der zu beobachtende parallele Rückgang von Pflanzen und Pollinatoren durch eine wechselseitige Spezialisierung erklären lässt. Wir untersuchten dazu 162 auf 119 Wiesen und Weiden unterschiedlicher Nutzungsintensität aufgenommene Pflanzen-Pollinatoren-Netzwerke in Hinblick auf ihre Stabilität. Das durch die Landnutzung bestimmte Schicksal einer Pflanzenart und des sie besuchenden Bestäubers waren eng miteinander verknüpft. Weiterhin hatte die Intensivierung der Landnutzung einen überproportionalen Einfluss auf die Abundanz spezialisierter Bestäuberarten. Die Abundanz spezialisierter Pflanzenarten nahm entlang des Landnutzungsgradienten nicht überproportional ab (Kapitel 3).

Die Intensivierung der Landnutzung scheint zu einem Rückgang der Pflanzendiversität zu führen, der wiederum zu einem ressourcenbedingten Rückgang der Bestäuberdiversität führt. Die durchschnittliche Reaktion der Pollinatoren auf die Landnutzung hat zwar auch einen Einfluss auf die Abundanz der von Ihnen besuchten Pflanzen, jedoch ist dieser Effekt weniger stark ausgeprägt. Netzwerkanalysen stellen somit ein geeignetes Werkzeug zur Charakterisierung mutualistischer Beziehungen

innerhalb von Artengemeinschaften dar. Sie können zur Vorhersage der Reaktion einer Artengemeinschaft auf Störung sowie der durch Artenverlust möglicherweise resultierenden Konsequenzen herangezogen werden.

Um herauszufinden, welche Aspekte der Landnutzung die Pflanzen-Pollinatoren-Beziehungen am stärksten beeinträchtigen, haben wir die Auswirkungen der Düngung, der Mahd und der Beweidung isoliert analysiert (Kapitel 4). Die Ergebnisse zeigten, dass sich die drei Komponenten in ihrem Einfluss auf den Artenreichtum und die Abundanz von Pflanzen sowie Pollinatoren zwischen den Exploratorien stark unterschieden. Während sowohl ein Anstieg der Düngeintensität als auch der Mahdhäufigkeit in zwei von drei Untersuchungsregionen mit einem Rückgang der Artenzahl bei den Pflanzen verbunden war, zeigten sich bei Artenreichtum, Abundanz und Komposition der Pollinatoren sowohl zwischen den Regionen als auch zwischen taxonomisch verschiedenen Pollinatorengruppen sehr unterschiedliche Trends.

Daher zeigen die Ergebnisse, dass es nicht ohne weiteres möglich ist, Schlussfolgerungen und Management-Empfehlungen von einer Region auf andere zu übertragen. Gleichwohl konnten wir auch hier zeigen, dass über alle Exploratorien hinweg das Schicksal der Pollinatoren durch die Reaktion der von ihnen besuchten Pflanzen auf die Landnutzungsintensität bestimmt wurde und umgekehrt (Kapitel 4).

Spezialisierte Pollinatoren wie beispielsweise oligolektische Bienen (Bienen, die nur den Pollen einer einzigen Pflanzenfamilie oder gar einer einzigen Pflanzenart sammeln) gelten häufig als anfälliger gegenüber äußeren Beeinträchtigungen und somit auch gegenüber Veränderungen im Ökosystem. Dies wird als Preis für die Spezialisierung angesehen – eine Hypothese, die durch meine Ergebnisse gestützt wird (Kapitel 3 und 4). Man geht davon aus, dass der Nutzen der Spezialisierung ihre Nachteile überwiegt. Bezogen auf Pollinatoren galt bislang, dass die Vorteile der Spezialisierung aus einer effizienteren Nahrungsaufnahme an den besuchten Pflanzen heraus resultieren. Dazu zählt neben zahlreichen weiteren Aspekten die Spezialisierung auf besonders nährstoffreichen Pollen.

Wir haben deshalb den Pollen von 142 Pflanzenarten gesammelt und die Zusammensetzung seiner Aminosäuren qualitativ analysiert. Die Zusammensetzung der Aminosäuren variierte stark zwischen den verschiedenen Pflanzenarten – nur bei taxonomisch verwandten Spezies waren große Ähnlichkeiten nachzuweisen.

Überraschenderweise erwies sich die Konzentration sowohl freier als auch protein-gebundener Aminosäuren – auch die der essentiellen – bei den Pollen liefernden Pflanzen, die von oligolektischen Bienen besucht werden, als deutlich niedriger, als bei anderen Pflanzen (Kapitel 5).
Des Weiteren wich die Zusammensetzung der Aminosäuren der Pollen bei den von oligolektischen Bienen besuchten Pflanzen stärker von der für Honigbienen optimalen Zusammensetzung essentieller Aminosäuren ab, als bei anderen Pflanzen. Das legt die Annahme nahe, dass Konkurrenzvermeidung oder anders gesagt der kompetitive Vorteil in Bezug auf die Pollenquantität dazu geführt hat, dass sich oligolektische Bienen auf Pflanzen spezialisiert haben, die Defizite in der Zusammensetzung ihrer Pollen-Aminosäuren aufweisen. Dieser Hypothese muss noch genauer nachgegangen werden.

Die Ergebnisse, die ich in dieser Dissertation präsentiere, werfen ein neues Licht auf die Interaktionsmuster zwischen Pflanzen und Pollinatoren und die daraus resultierenden Konsequenzen. Konträr zur derzeit vorherrschenden Meinung zeigen wir auf, dass die Interaktionen zwischen Pflanzen und Pollinatoren ein hoch spezialisiertes System bilden, in dem die Diversität von Pflanzen und Pollinatoren stark voneinander abhängt.

Bumblebee approaching *Rosmarinus officinalis (Hummel im Anflug auf Rosmarinus officinalis)* © Christiane N. Weiner

1. General introduction

1.1 Why study biodiversity and ecosystem functions?

Biodiversity, a term coined by E. O. Wilson in the late eighties, describes the number and variety of living organisms, at all levels ranging from genetic diversity within a species to the variety of ecosystems on Earth. Moreover, biodiversity is a factor crucially modifying ecosystem function. Numerous studies, mostly for experimental grassland systems, demonstrated that ecosystem properties such as stability, fertility or susceptibility to invasion greatly depend on it (Hassan et al. 2005). For example, species-rich soil communities show enhanced litter decomposition compared to species-poor ones and consequently meliorate soil formation (Bradford et al. 2002). Species-rich plant communities show higher stability and resilience towards drought as well as higher productivity resulting in augmented carbon storage (Tilman and Downing 1994, Tilman et al. 1997) and high pollinator richness leads to improved seed set in some crops and wild flowers (Klein et al. 2003). Biodiversity thus directly and indirectly supports the provision with ecosystem goods and services (Figure 1).

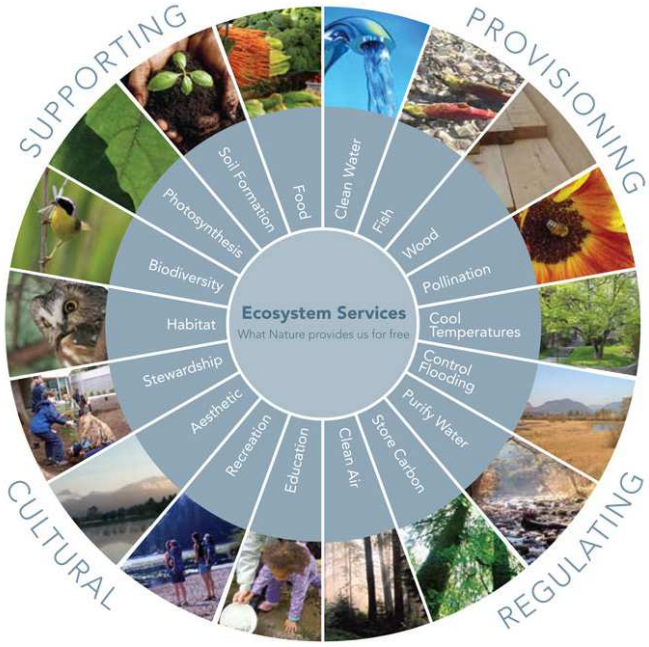

Figure 1: An overview of ecosystem services (source: www.metrovancouver.org)

In addition to goods such as fresh water, fiber or fuel (provisioning services), which are directly obtained from ecosystems, regulating services like pollination as well as supporting and cultural services gained increasing attention. They are obtained only if ecosystems include the biodiversity that guarantees the functional processes necessary to underpin them (Daily 1997, Hassan et al. 2005). However, the mechanism by which diversity of organisms influences ecosystem functioning is poorly understood (Yachi and Loreau 1999, Hooper et al. 2005). Biodiversity research is still in its infancy when

it comes to the question how sundry components of biodiversity are linked to the provision of ecosystem services or create resilience to environmental change (Rands et al. 2010). However, it is uncontroversial that alterations of species composition and loss of species have far-reaching consequences for each ecosystem and for many aspects of human welfare, pre-eminent economical ones. Thus, the ongoing and recently accelerated global declines in biodiversity have given new prominence to questions concerning the relationship between human activities, biodiversity and the stability of fundamental ecosystem functions and services (Rands et al. 2010). We thus need to address the mechanism by which biodiversity influences stability and resilience of ecosystems to predict the consequences of biodiversity loss and educe suitable nature conservation strategies.

In terrestrial habitats overexploitation, degradation, habitat disruption, introduction of alien species, fragmentation, climate change and agricultural intensification are the main reasons why nowadays human activities are considered the main cause of biodiversity loss (Butchart et al. 2010, Krauss et al. 2010, Bellard et al. 2012). While for some taxa, namely vertebrates, vascular plants and some invertebrate groups such as grasshoppers and butterflies, the existence of a negative correlation between agricultural intensification and biodiversity is satisfactorily proven, it is unknown for others (Fischer et al. 2010). In addition, it often remains unclear if land-use intensification affects biodiversity directly or indirectly and which effect individual elements have within land-use practices. But undoubtedly it poses a serious risk to biodiversity preservation and ecosystem services.

As almost two thirds of all hitherto described species are insects and about one sixth are flowering plants, terrestrial ecosystems are dominated by the interactions of these two groups (Waser and Ollerton 2006). With regard to ecosystem services they play a major role in pest control, pollination and above all for our food provision (Kremen and Chaplin-Kramer 2007).

To achieve the projected global food demand by 2050, particularly grasslands, which cover more than 36 per cent of the global land surface, are predicted to undergo rapid intensification (Asner et al. 2004, Tilman et al. 2011). However, replicated large-scale investigations on the characteristics and fragility of multi-species networks and

ecosystem functioning in such real ecosystems facing agricultural intensification are basically lacking. Studies undertaken on the topic so far focus mostly on few species and use coarse qualitative categorization of land-use intensities (Fischer et al. 2010). Theoretic modelling of biodiversity change, stability and resilience of ecosystems has outcompeted experimental work, especially field research, by far. However, only field experiments combined with ecosystem monitoring may actually assess temporal stability and response to as well as recovery from disturbance (Hooper et al. 2005).

My dissertation focuses on the mutualistic interactions between flowering plants and flower-visiting insects and their interactive response to human activity in relation to the fundamental aspects of biodiversity that underpin the ecosystem service of pollination.

1.2 Facts and considerations about mutualistic plant-flower visitor interactions

1.2.1 The beginnings of pollination biology

Nowadays it is a matter of common knowledge that flowers are frequently visited by insects and that both, flowers and visitors, may benefit from this relationship. While – concerning ideal mutualistic interactions – insects visit flowers to consume pollen or nectar, flowers in turn profit by being pollinated. Joseph Gottlieb Kölreuter (1761) was the first to fully recognize that pollination in many flower species does not result only from wind as hitherto believed, but from flower-visiting insects. His successor, Christian Konrad Sprengel (1793), convinced of the intentional design of flowers for pollination either by insects or wind, described the features of flowers in painstaking detail. His observations of plant-insect interactions and his hypotheses on the function of flower structures and colors as signals established the basis for pollination research (Waser 2006). However, it was not until Darwin (1859) that the study of pollination was put into its modern evolutionary context. As the interests of plants and pollinators naturally differ (improvement of reproductive fitness vs. maximum efficiency in nutrient acquisition), Darwin argued that the complex morphology of some flowers as well as dichogamy and obligate out-crossing by insect pollination resulted from

adaptation by natural selection and co-evolutionary processes in plants and flower-visitors. Since then, scientists all over the world have tried to shed light on different aspects of the complex relationships between plants and flower-visitors.

1.2.2 The value and endangerment of pollination as an ecosystem service

As noted above plant-flower visitor relationships involve pollination and thus one of the most important ecosystem services. This service is not only crucial for the ecological process of seed set and plant reproduction in the wild, but also for crop production and thus for human welfare. About 87.5 per cent of angiosperms depend on animal pollination and roughly 75 per cent of our main food crops show increased fruit or seed set when animal pollinated (Ollerton et al. 2011). Alike other ecosystem services pollination is not compensable by technology to any considerable degree. Consequently, pollination worries rise as honey bees and other pollinators decline. In the USA alone the annual economic value of pollination services provided by wild and managed pollinators was estimated to US $ 1.6-5.7 billion for honey bees and US$ 4.1-6.7 billion for other pollinators (Southwick and Southwick 1992). Simpler calculations which did not take into account that wild pollinators may replace honey bees in providing pollination service to several crop species, even estimated the value of honey bee pollination to $ 8.3 billion (Robinson et al. 1989) and $ 14.6 billion respectively (Morse and Calderone 2000).

The global decline in honey bee colonies implies that wild pollinators will play an increasingly important role in crop pollination carried out formally by honey bees. However, the pollination service provided to cultivated crops by wild and managed pollinators requires suitable foraging and nesting habitats adjacent to croplands (Kremen et al. 2002, Klein et al. 2007, Jauker et al. 2009). For example, solitary bees including oligolectic species only undertake short distance flights of no more than 150-600 m around their nesting sites for pollen collection (Gathmann and Tscharntke 2002). Moreover, numerous pollinators, i.e. butterflies and oligolectic bees are known to be strongly dependent on certain plant species and nesting materials for oviposition and larval development (Johst et al. 2006, Praz et al. 2008). Thus, not surprisingly, the response of wild bees to habitat loss strongly depends on their diet breadth and dispersal ability (Bommarco et al. 2010). On the other hand, one has to take into account that, as

many wild pollinators are endangered, with their loss more specialized plant species may be threatened as well. The goal of yield maximization pursued by modern agriculture has led to a fundamental increase in land-use intensity followed by a radical decline in agro-biodiversity. An ample availability of pollinators at the right place and time, can no longer be taken for granted (Nabhan and Buchmann 1997).

It has been documented that habitat degradation and fragmentation (Jennerston 1988, Rathcke and Jules 1993, Aizen and Feinsinger 2003, Krauss et al. 2010), the use of agrochemicals (Johansen 1977, Desneux et al. 2007, Barmaz et al. 2010, Barmaz et al. 2012), introduced pests and competitors (Roubik 1978, Goulson 2003), as well as land use and climate change may lead to diversity loss, reduced pollinator visitation or disruption of plant-pollinator interactions resulting in reduced fruit or seed set in plant populations (Cunningham 2000, Klein et al. 2003, Aguilar et al. 2006, Schweiger et al. 2008, Schweiger et al. 2010).

There is an urgent need to understand how plant-pollinator communities respond to land use and changes in management in order to be able to elaborate adequate implications for management and protection. Otherwise, the ecologically and economically valuable complex interactions between plants and their pollinators, some of which may have taken ages to evolve, might be lost irretrievably.

1.2.3 Specialization and generalization in plant-flower visitor interactions

Plant-flower visitor interactions are regarded as one of the driving forces having fostered the adaptive radiation of angiosperms to the present level of plant diversity (Muchhala et al. 2010). They represent one of the most popular examples of how enduring reciprocal selective pressure can lead to co-evolutionary races and rapid evolutionary change (Fenster et al. 2004, Lunau 2004). However, in most cases the underlying co-evolutionary system is diffuse and co-adaptation cannot be attributed to specific coevolving species (Lunau 2004). Hence, plant-flower visitor relationships range from highly specialized interactions between pairs of closely coevolved species to broadly generalized, loose and randomly appearing associations.

Before analyzing the effect of land-use intensity on diversity and species composition of plant – flower-visitor interactions, it is therefore necessary to check how much the different species rely on each other. Depending on how high the degree of specialization

is, mutualistic networks are supposed to vary in their susceptibility to disturbance and to secondary extinctions of species. Thus, the characterization of specialization and generalization is important for the general understanding of ecosystems and their endangerment.

1.2.3.1 Niche theory

Characterization of generalization and specialization may be conducted based on the niche concept. A fundamental niche as defined by Hutchinson (1957) is an n-dimensional hypervolume, where the dimensions correspond to the range of physical and biological environmental conditions and the resources that define the requirements of a species. Typically, a species' realized niche, i.e. the range of environmental conditions and resources it actually uses, is narrower than the fundamental niche due to inter-specific interactions like predation and competition (Begon et al. 1990). As long as a habitat offers conditions and resources matching a species' niche, this species may persist there, if not forced out by competitive interactions. On the other hand, if ecosystem change results in conditions and resources not meeting a species' niche, the species either needs to adapt to its new environment or will face extinction (Holt 2009, Colwell et al. 2012).

Specialists, i.e. species inhabiting narrow fundamental niches regarding one or more dimensions, are usually considered to be more vulnerable to disturbance than generalists. It is broadly believed that the narrowness of their fundamental niche limits their ability to cope with sudden or quickly progressing ecosystem changes (e.g. McKinney 1997, Owens and Bennett 2000). Coherently, species confined to limited resource diversity, i.e. inhabiting narrow niches concerning resource use, were hypothesized to be particularly vulnerable to disturbance, too. However, this assumption requires that species are affected indirectly via their resources and not directly via increasing mortality (Vázquez and Simberloff 2002).

Considering flower visitors, flowering plants represent important food sources, and under certain conditions, shelter. Thus, flowers are an important component of a flower visitor's niche. Conversely, pollinators represent an important resource for plants in terms of reproductive fitness and thus a component of their niche (Vázquez and Aizen 2006).

As in the context of studying real ecosystems the assessment of specialization and generalization in most cases will be based on realized niches rather than fundamental ones, predictions on species vulnerability have to be handled cautiously. While, for example some highly pollinator-specialized plant species fail to reproduce if introduced to alien habitats, others may be pollinated effectively by a variety of non-native species (Armbruster and Baldwin 1998, Richardson et al. 2000). Nevertheless, resource-based mechanisms may play an important role for ecosystem stability, particularly in highly specialized interactions (Blüthgen et al. 2007).

1.2.3.2 Specialization metrics

Network analyses provide a valuable tool for characterizing patterns of mutualism, specialization and generalization in a community context (Montoya et al. 2006, Blüthgen 2010). Theoretically, they may be employed to predict community responses to disturbance and possible consequences of species loss. Network metrics enable us to estimate how dependent co-occurring species are on one another (Blüthgen et al. 2007). However, for multiple reasons shortly outlined below, the deduction of unbiased specialization values from species interaction webs refuses to be ordinary. Depending on the method it is even highly problematic.

Traditionally, one of the most common methods to evaluate specialization was to simply count of the number of links, i.e. inter-specific interactions a species has, also called “species degree” (Jordano 1987, Vázquez 2005). One crux of this method is that it does not allow distinction between species displaying the same number of links, but differences in quantitative link importance i.e. in interaction strength. The same is generally true for all other unweighted network metrics (connectance, nestedness, degree distribution). If one species interacts with three species in equal frequency but another species interacts with three interaction partners strictly preferring one of them, this undoubtedly makes a difference in the ecological impact the species may have on one another (Blüthgen 2010) and should not be ignored. Thus, purely qualitative network metrics provide only rough information on niche breadth and interdependence of interacting species.

Another crucial point is that most network indices do not account for differences in sampling effort (Blüthgen et al. 2008, Dormann et al. 2009, Blüthgen 2010). If a species has been observed frequently and another one just a few times, it is not surprising if the frequently observed one may display more links. In this case it is logically impossible to distinguish if differences in species degree derive from sampling limitation or from real specialization, especially if a species was observed just once (Blüthgen et al. 2008, Blüthgen 2010). In fact, many ecological networks display a strong correlation between observation frequency and number of links (Vázquez and Aizen 2003). Thus, the number of links and metrics based upon it should not be applied without correction for total observation frequency if trying to analyze dependence and niche breadth in species networks.

To largely circumvent the problems outlined above, the specialization measures d' and H_2' can be used (Blüthgen et al. 2006). H_2' characterizes the network level of specialization based on the complementarity and exclusiveness of observed interactions in comparison to a neutral quantitative network i.e. a probability distribution of interactions based on observed interaction totals. Conversely, H_2' depicts niche partitioning across species. d' characterizes niche breadth based on a species' deviation e.g. in flower visitation from the neutral distribution of all flower visitors (Blüthgen et al. 2006).

Both metrics range from 0 to 1, with high values indicating complementary specialization. Highest specialization is assigned to the most unexpected scenario, e.g. each pollinator species visiting a plant species not visited by anyone else. Due to the null-model based correction, the indices are virtually unaffected by variation in sampling effort and total interaction frequency (Blüthgen et al. 2007, Blüthgen 2010). However, as they consider interaction probability, these metrics cannot detect asymmetric specialization, e.g. a rarely observed pollinator specialized on the most commonly visited plant species, as this corresponds to the expected neutral distribution (Blüthgen 2010).

1.2.3.3 Reasons for and consequences of specialization in plant-flower-visitor networks

Most flower visits from insects do not occur haphazardly, but intended (Cane and Sipes 2006). Indeed, plant-pollinator networks are even very specialized in comparison to other plant-animal interactions (Blüthgen et al. 2007), although the vast majority of pollinators visits multiple plant species and most plants are visited by multiple flower-visitors (Waser et al. 1996, Fenster et al. 2004).

From the plants' point of view, specialization is easy to understand. Plants need to maximize their reproductive output at minimal own resource cost, so at minimal loss of pollen and nectar. The evolution of complex flowers, pollination syndromes and highly specialized pollination mechanisms can be explained by the fact that flower visitors vary in their beneficial effects on plants. This variation in effect constitutes one of the primary conditions required for the specialization of plants on pollinators (Schemske and Horvitz 1984). While uncompromising specialization on specific pollinator species is rare, evolutionary selection and diffuse coevolution are supposed however, to favor morphological or chemical floral traits – also referred to as floral filters – that minimize reproductive costs by inviting advantageous and excluding undesirable flower-visitors (Junker and Blüthgen 2010). Extraction of pollen without pollination as well as nectar robbing, illustrate antagonistic interactions which have to be suppressed. Specialization thus increases the probability of pollen being transferred among conspecific flowers, simultaneously reducing the risk of pollen being wasted on alien flowers or alien pollen blocking conspecific stigmas (Fenster et al. 2004, Muchhala et al. 2010). Yet, in plant species whose visitation rates are very low, generalization is favored as it reduces the amount of undispersed pollen in the anthers (Muchhala et al. 2010).

Flower visitors need to maximize their nutrient intake at minimal energy loss. Thus, from the flower visitor's point of view specialization is somewhat more difficult to understand as it may hamper an animal's ability to cover its nutritional requirements. While generalized flower visitors spread their risk of extinction on several resources, in specialists it is concentrated on one or few (Den Boer 1968). Specialization in pollinators thus was associated with potentially high costs. Conversely, several hypotheses have been stated which claim that advantages from specialization may outweigh its costs. These comprise higher foraging efficiency from morphological,

physiological or behavioral adaptation, avoidance of competition by specialization on toxic resources and specialization on very nutrient rich resources (Strickler 1979, Dobson and Peng 1997, Budde et al. 2004, Müller and Bansac 2004).

On the basis of a comparison of recent and historical data from England and the Netherlands Biesmeijer and colleagues (2006) showed parallel declines in pollinators and insect-pollinated plants. The obvious question is, whether a causal relationship exists. A decrease in floral resources could lead to the disappearance of flower visitors and vice versa. However, this assumption requires that species are interdependent.

For butterflies it is well documented that the loss of species-specific larval host plants entails co-extinctions (Thomas et al. 2001, León-Cortés et al. 2003, Koh et al. 2004a, b, Krauss et al. 2004) and that agricultural land use, e.g. mowing, causes losses in species diversity via life-cycle disruption (Johst et al. 2006). Likewise, an unconditional dependence on host plants was shown for some oligolectic bee species that fail to develop on non-host pollen (Praz et al. 2008). These results underpin the theory that species inhabiting narrow resource niches are prone to disturbance and that resource specialization and resource availability play a major role for the diversity and persistence of plant-flower visitor communities in a given ecosystem. Moreover, it may be expected that species are affected by land-use related changes in their resources dependent on their degree of resource specialization (Koh et al. 2004b).

If, due to mutual specialization, flower-visitors are found to be highly dependent on flower diversity, this would mean that a decrease in resources could lead to a parallel decline in the biodiversity of consumers (Colwell et al. 2012). Moreover, changes in resource composition could entail shifts in species composition of consumers, eventually resulting in the loss of specialists and a functional homogenization at the community level (Clavel et al. 2010, Filippi-Codaccioni et al. 2010).

Doubtless, the species within a flower-visitor population differ concerning their flower preferences and diet breadth (e.g. Goulson and Darvill 2004, Tudor et al. 2004). Imagine a continuum of resource – consumer interactions ranging from broadly generalized to highly specialized ones. On the one end, consumers do not display any morphological, physiological or behavioral constraints regarding their resources.

Theoretically, such consumers adapt easily to new resources and may even profit from using multiple resources. Moreover, they do not suffer from resource-mediated declines in diversity or abundance as long as the overall resource supply serves their nutritional requirements.

On the other end of the continuum consumers are strictly confined to specific resources either by morphological, physiological or behavioral constraints, and cannot adapt to changing environmental conditions as easily as generalists. If a certain pollinator species is restricted to one floral resource and this resource declines in abundance or disappears from the ecosystem due to changes in environmental conditions the pollinator will decline or disappear from the ecosystem accordingly if it is unable to switch to other resources.

Vice versa, a given plant species, albeit visited by several flower visitors, may suffer from pollinator loss or pollen limitation if residual flower visitors do not pollinate, e.g. due to morphological constrains.

In my thesis we employed plant-pollinator interaction networks to explore the diversity and specialization of flowers and flower visiting insects along a gradient of increasing land-use intensity in grasslands. We aimed to examine the relationship between niche properties and species sensitivity to disturbance, i.e. land use and which land-use components exert the most profound impacts on the diversity of plants and pollinators. Additionally, we focused on reasons for resource specialization of bees.

1.3 The Biodiversity Exploratories

The idea behind the Biodiversity Exploratories project was to install a large-scale and long-term platform for investigation of biodiversity and ecosystem functioning. More specifically, the Biodiversity Exploratories were set up to observe human-induced changes in biodiversity and to evaluate the impacts of those changes for ecosystem processes. The Biodiversity Exploratories are located in three different geographical regions: Schorfheide-Chorin (Brandenburg, NE Germany), Hainich-Dün (Thuringia, Central Germany) and Schwäbische Alb (Baden Württemberg, SW Germany) (Figure 2, Fischer et al. 2010). Each Exploratory covers an area of 422 km up to approx. 1300 km² and comprises 50 grassland plots (50 × 50 m) which are randomly distributed neighboring arable fields, forests and settlement areas. The represented land-use types range from near-natural, protected sites to intensively fertilized, mown or grazed meadows and pastures (sheep, horses, cattle). In addition to these differences in agricultural management, differences in climate, soil types, formation history and topography promote regionally different diverse vegetation. In the Schorfheide region precipitation is very low (500-600 mm) and soil types include albeluvisols, cambisols, gleysols, histosols and luvisols, whereas in the Hainich precipitation is intermediate (600-800 mm) and soil types are dominated by cambisols, stagnosols and vertisols. In the Alb precipitation is high (700-1000 mm) and soil types include leptosols and cambisols. Thus, the three Exploratories enable the investigation of land-use impacts on plant-pollinator interactions under very different abiotic and biotic conditions.

Figure 2: Geographic location of the three Biodiversity Exploratories in Germany

1.4 Thesis outline

The major aim of my thesis was to explore the diversity and specialization of flowers and flower-visiting insects along a gradient of increasing land-use intensity in grasslands. Moreover, we aimed to explore how the land-use response of a species may influence its interaction partners. We focused on how niche- and resource-based mechanisms determine the composition and specialization of plant-pollinator communities and resource preferences of flower-visitors.

In my thesis I addressed the following subjects:

1. **Effects of mowing and fertilization on diversity, composition and specialization of plant-flower visitor interactions on meadows**

   To explore how increasing land-use intensity affects diversity and composition of plant-flower visitor interactions on meadows, we compared meadows managed at low and high intensities. We employed a network approach to test whether specialization and complementarity of flower visitors differed between management types.

2. **Effects of quantitative land-use intensity and specialization on mutualistic interactions**

   To study if land-use related parallel declines in plants and pollinators may result from mutual specialization, we analyzed 162 plant-pollinator networks from 119 grassland sites managed at different intensities. We aimed to explore natural community responses to land-use, i.e. how the land-use response of one species influences its interaction partners, and to predict possible consequences from specialization.

3. **Response of plant-pollinator networks in relation to management practice**

   To investigate how plant-pollinator networks respond to differences in management techniques and intensification within different management types, we conducted isolated analysis of mowing, grazing and fertilization on plant-pollinator networks.

4. Resource choice of flower visiting insects in relation to pollen quality

As I hypothesized that pollinator specialization may increase with the nutritional quality of pollen offered by a flower, I analyzed 142 plant species for their qualitative and quantitative amino acid composition and tested whether pollen protein content and composition plays a role in the host plant selection of oligolectic bees.

2. Effects of meadow management on diversity, composition and specialization of plant-flower visitor interactions

This chapter has been published as:
Weiner, C.N., Werner, M., Linsenmair, K.-E., Blüthgen, N. (2010): Land-use intensity in grasslands: changes in biodiversity, species composition and specialization in flower-visitor networks. Basic and Applied Ecology 12 (4), 292-299.

Summary

The relationship between resource availability and biodiversity of consumers has gained particular attention with the increasing loss of biodiversity. We evaluated resource availability on meadows of low intensity (low/unfertilized, mown once or twice per year) and meadows of high intensity land use (high fertilization, mown twice or trice) before and after the first mowing in relation to network specialization, species richness and composition of flower visitors.

We studied 40 meadows, simultaneously sampling one meadow of low intensity and one meadow of high intensity land use. Each survey yielded a separate interaction network, comprising all flower-visitors found during 6 h in an area of 1000 m^2.

In total we recorded 105 plant species and 586 flower-visitor species. Species composition of plants and flower visitors differed considerably between the two management regimes, with species overlaps of 43 % in plants and 42 % in flower visitors. Complementary specialization of flower visitors differed between taxa: dipterans were significantly less specialized than beetles and butterflies, and bees had the highest degree of specialization. Earlier in the season (before mowing), meadows of low intensity land use were significantly richer in plant, bee and butterfly species. They also showed more plant-flower visitor interactions, greater flowering areas and higher individual numbers of butterflies than meadows of high intensity land use. However, later in the season (after mowing) management types differed only in plant species richness, being higher on meadows of low intensity land use.

We conclude that variations in plant species composition resulting from differences in grassland management may alter plant-flower visitor interactions. Moreover, an impoverishment of flower diversity has stronger effects on the diversity and species

composition of specialized flower visitor groups than on little or unspecialized flower visitors.

2.1 Introduction

The determinants of biodiversity are a key question in ecology which deserves particular attention in the face of the rising loss of species in recent decades (Ehrlich and Wilson 1991, Allen-Wardell et al. 1998). Species richness, but especially functional diversity, may enhance ecosystem stability and resilience (Naeem and Li 1997) and also determine the performance of ecosystem processes (Tilman et al. 1997). Thus, the maintenance of ecosystem services such as pollination will require a better understanding of each species' role and how species losses may affect them (McCann 2000, Loreau et al. 2001, Memmott et al. 2004, Fontaine et al. 2006).

Despite of the declines in honey bees and wild bees reported from the US and Europe a general "pollination crisis" is still being controversially discussed (Ghazoul 2005, Steffan-Dewenter et al. 2005, Biesmeijer et al. 2006, Aizen and Harder 2009). Several studies have shown that pollinator visitation and diversity may be negatively influenced by habitat degradation and fragmentation (Rathcke and Jules 1993, Cunningham 2000) as well as by agrochemicals (Johansen 1977, Crane and Walker 1983, Kevan and Phillips 2001). Mowing may affect pollinators via changes in resource supply, and its timing and frequency markedly alter species composition (Fenner and Palmer 1998). Moreover, mowing causes temporary declines in the diversity and abundance of many insect species and may limit their reproduction by harming the larvae (Johst et al. 2006). Losses in pollinator diversity or abundance may lead to a reduced seed set in plants (Jennerston 1988, Klein et al. 2003). Parallel diversity declines in insect-pollinated plants and in pollinators were reported from Britain and the Netherlands (Biesmeijer et al. 2006). Still it is unclear, if one decline causes the other or if both groups are adversely affected by a third factor. Ebeling et al. (2008) showed that reduced flower diversity causes reduced pollinator abundance and diversity in small scale experimental plots. Thus, it is conceivable that declines in plant diversity, as e.g. caused by land-use intensification may cause declines of flower visitor diversity due to mutual specialization and vice versa. High soil nitrogen levels due to fertilization are known to

affect floral abundance and composition reducing plant diversity and favoring the biomass of grasses (Suding et al. 2005, Burkle and Irwin 2009). On the contrary, low nitrogen levels favor forbs and thus flower production and pollinator visitation (Burkle and Irwin 2010).

We focus on specialization, diversity and composition of plant-pollinator networks on two meadow types that differ in management intensity. As plant-pollinator networks show a high seasonality (Olesen et al. 2008) this can override effects of land-use intensity on a flower-visitor community. We therefore used a standardized pair-wise sampling design which allowed comparing simultaneously recorded meadows differing in land-use intensity, but not in season or weather conditions. However, meadows of high land-use intensity are often mown earlier than ones of low land-use intensity, which may affect the state of regrowth. We thus expected clearer management effects before than after mowing.

We hypothesized that (1) flower diversity and abundance decrease with increasing land-use intensity, and that (2) this trend is associated with a decline in diversity and abundance of flower visitors. A decline in consumers may be a response to impoverished resource availability. In particular, (3) stronger effects of flower diversity on visitor diversity are expected when the latter are more specialized. Hence, specialization and complementarity of flower visitor interactions were examined using a network approach and quantitative metrics.

2.2 Methods

2.2.1 Data collection

Between May and August 2007, we investigated a total of 40 grassland plots (20 plots of high and 20 of low intensity management) in Schwäbische Alb, south-western Germany. Plots were selected from a pre-selection of 1000 plots for which information on land-use type was available as part of the Biodiversity Exploratories Project (www.biodiversity-exploratories.de). Flower visitors were recorded simultaneously on meadows of low land-use intensity (hereafter called low-IM) and meadows of high land-use intensity (hereafter called high-IM), thus comprising a pair-wise design. Low-

IM were unfertilized or in two cases low fertilized (50/60 kg N/ha), while in high-IM the fertilization level varied from 80 – 450 kg nitrogen/ha with a median level of 80 kg N/ha. For the low-IM that were mown only once, the mowing date was in mid-July, whereas two low-IM were mown in Mid-June and late August. In high-IM, which were mown 2-3 times a year, the date of the first mowing was in mid-June to mid-July, the second mowing followed in mid or late August, and in some a third mowing occurred in late September or October. In our late season sampling ("after mowing") all types of meadows were surveyed after their first mowing. Pairs of meadows were chosen to have soil conditions and plot surroundings as similar as possible. Species composition of plants and flower visitors was not influenced by the spatial distance between the meadows (Mantel test, plants: $r = 0.08$, $p = 0.075$; insects: $r = 0.004$, $p = 0.468$; based on Bray-Curtis distance and 10^5 permutations). Each meadow was surveyed for six hours between morning and afternoon and each survey comprised a meandering transect walk of 333 m length and 3 m transect width covering an area of approx. 1000 m^2 per plot. Ten pairs of meadows were sampled before their first mowing (May to mid-July) and ten pairs approximately 3-8 weeks after their first mowing (late July to late August). We counted the flowering units per plot for all flowering plant species (excl. grasses), or, in highly abundant species, estimated it by extrapolation from a small area. A 'flowering unit' was defined as a unit of one (e.g. Geraniaceae) or more flowers (e.g. Asteraceae, Apiaceae) demanding insects to fly for getting from one unit to another (Dicks et al. 2002).

Diversity of flowers was calculated after multiplying the number of flowering units of a species by its average flowering area in cm^2 to account for differences in flowering area. This was done because the size of the flower display relates to pollinator attraction (Vaughton and Ramsey 1998). Additionally, we found a positive relationship between flowering area and pollen volume per flower (Pearson, $p = 0.00002$, $r = 0.62$, $N = 40$; unpublished data). In actinomorphic flowers flowering area was calculated as a circle based on the flower diameter, whereas the flowering area of zygomorphic flowers was calculated as a rectangle based on flower length and width. As in umbels the parts of a flowering unit are standing together rather loose compared with actinomorphic flowers, their diameter was divided by two before calculating their flowering area.

All insects that visited flowers were registered as well as the plant species on which they were observed, disregarding only those insects which were sitting on the outer petals and obviously not feeding on pollen or nectar. Specimens that could not be identified in the field were collected using a sweep net. They were kept in alcohol vials, sorted and identified to species level where possible. Thysanoptera were not captured as they are easily overlooked and thus may create a bias for some plants if collected erratically. For each of the surveyed plots we calculated a separate interaction network.

2.2.2 Statistical analysis

Statistics were conducted in R 2.8 (R Development Core Team 2008). Contrasting most previous studies each of our recorded plant-flower visitor networks was analyzed separately. By using only short-term interaction networks we avoid seasonal variation and non-overlapping phenologies.

Complementary specialization of flower visitors was calculated using the indices d_i' and H_2' (Blüthgen et al. 2006). Unlike previous approaches, the results are not biased by variation in total interaction frequency and sampling effort (Blüthgen 2010). The index d_i' describes the species' deviation in flower visitation from the distribution of all visitors. H_2' characterizes the degree of complementary specialization in the entire network (compare Blüthgen and Klein 2011). For both measures high values indicate strong niche partitioning and specialization.

For each of the most abundant flower visitor groups, namely bees, beetles, butterflies, hoverflies, and other dipterans we calculated a weighted mean d_i' per plot. The measure d_i' was weighted by the species total interactions, but excluding species observed only once. Repeated measures ANOVA (type III, with land use as repeated measure to account for the pair wise sampling design) followed by a Tukey post-hoc test was conducted to examine differences in specialization of flower visitor groups. As homogeneity of variance among the different flower visitor groups could not be achieved for the full data set, we excluded the groups with the highest variances, Lepidoptera and Coleoptera, and conducted a second ANOVA on the reduced data set where variance homogeneity was achieved. Differences between the pollinator groups stayed highly significant ($p < 0.0001$), confirming the results for the full data set presented below.

Plant and flower visitor diversity and evenness were calculated based on Simpson's diversity

$$D = 1/\sum p_i^2 \qquad \text{and} \qquad E = \frac{D-1}{N-1}$$

where p_i is the proportional abundance of each flower visitor i from the total abundance of N flower visitors. Additionally we compared plant and flower visitor species richness that was rarefied to the lowest common denominator of all plots (i.e. to 382 flower units and to 160 individual visitors per plot) using the EcoSim package and 1000 iterations (Gotelli and Entsminger 2009).

We tested the relationship between floral availability and responses of visitors, first correlating flowering area and total number of flower visitors per plot. To determine the relationship between flowering area and interaction frequency at the species level, we calculated linear correlations between log(number of interactions per plant species) and log(flowering area) across all plant species per network and then quantified the combined mean effect size from all 40 networks by using standard meta-analysis tools (MetaWin 2.0; Fisher's z-transformation, sample size as richness of plant species, fixed effect; 95% confidence intervals were based on bootstrapping with 999 iterations, bias-corrected).

Insect diversity calculations comprised all individuals identified to species level plus all individuals belonging to groups which generally could be identified only to a cruder taxonomic level: 512 (3.6 %) visitors, determined to family (283 individuals, 25 families) or genus level (238 individuals, 40 genera). These groups did not contain any of the identified species, so they added to overall diversity. Removing these cases from the analysis did not affect the overall results. However, for analyses of specialization (H_2', d_i'), these cases were excluded.

Two-tailed paired *t*-tests were conducted to examine whether management types differed in diversity, abundance and rarefied species richness of plants and pollinators, or network specialization. Where necessary, we used logarithmic transformation to approach a normal distribution.

To analyze differences in species composition between management types, permutational multivariate analyses of variance using distance matrices ("Adonis"

command, R-package vegan 1.17-1 (Oksanen et al. 2008), based on Bray-Curtis distances and 10^5 permutations were conducted. This is a robust technique (Oksanen 2010) that allows partitioning of distance matrices among sources of variation and uses F-tests based on sequential sums of squares from permutations of the raw data to assess statistical significance.

We tested species composition of plants, bees, hoverflies, butterflies, beetles and dipterans as well as all flower-visitors combined. These calculations were based on relative abundances to eliminate confounding effects of variation in total abundance. However, calculations based on total abundances and Jaccard's distances yielded the same overall results.

2.3 Results

In total we recorded 105 plant species and at least 586 flower-visitor species. Ninety-four plant species were found on meadows of low land-use intensity (low-IM) and only 56 species on meadows of high land-use intensity (high-IM). Plant species overlap between land-use types was 45 species (43 %). The number of flower visitor species amounted to 402 species on low-IM and 433 species on high-IM, with 249 species occurring in both management types (42 %). Species composition was significantly different between low-IM and high-IM for plant and bee species, and marginally significant for butterflies and total flower visitors (Table 1) although land-use type explained only 3-11 percent of the total variation. Syrphids, other dipterans and coleopterans did not show significant compositional differences related to management types. Species composition of all taxa was highly related to season (before vs. after mowing, Table 1).

Table 1: Comparison of relative species composition on meadows of low and high land-use intensity, based on Bray-Curtis dissimilarity matrices and permutational multivariate analysis of variance ("Adonis" procedure in the vegan package, df = 1, 9999 permutations) across all plots. Clustering was partly significant although season (before vs. after mowing) and land-use type explained just 3-19 percent (R^2) of total variation.

	Factor	*R²*	*F*	*p*
Plants	M	0.12	5.54	0.0001
	LU	0.11	5.17	0.0001
All flower visitors	M	0.14	6.14	0.0001
	LU	0.03	1.44	0.0589
Apidae	M	0.10	4.14	0.0005
	LU	0.04	1.69	0.0471
Coleoptera	M	0.19	9.33	0.0001
	LU	0.03	1.46	0.1804
Lepidoptera	M	0.07	2.94	0.0007
	LU	0.04	1.58	0.0834
Syrphidae	M	0.13	5.97	0.0001
	LU	0.03	1.32	0.2118
Diptera	M	0.12	4.97	0.0001
	LU	0.03	1.32	0.1273

Low-IM were richer in flowering plant species both before (paired t-test, $t = 4.13$, $p = 0.003$, n = 10 plot pairs) and after mowing ($t = 2.65$, $p = 0.027$, n = 10) than high-IM (Figure 3). Tests using rarefied species richness yielded the same trends (before mowing: $t = 2.71$, $p = 0.024$; after: $t = 2.21$, $p = 0.054$). Simpson's diversity and evenness based on flowering area did not differ between the management types before or after mowing (all $t \leq 1.77$ $p \geq 0.11$, Figure 3). Neither did number of flowering units (all $t \leq 1.42$ $p \geq 0.19$). However, flowering area was higher on low-IM compared to high-IM before mowing ($t = 2.32$, $p = 0.043$) but not afterwards ($t = 1.45$, $p = 0.18$). Across all plots, flowering area and visitor numbers did not correlate ($t = -0.19$, $p = 0.85$, $n = 40$), but visitation and flowering area of each plant species within each network correlated positively (meta-analysis: mean $r = 0.65$, 95% CI 0.61 - 0.69, n = 40).

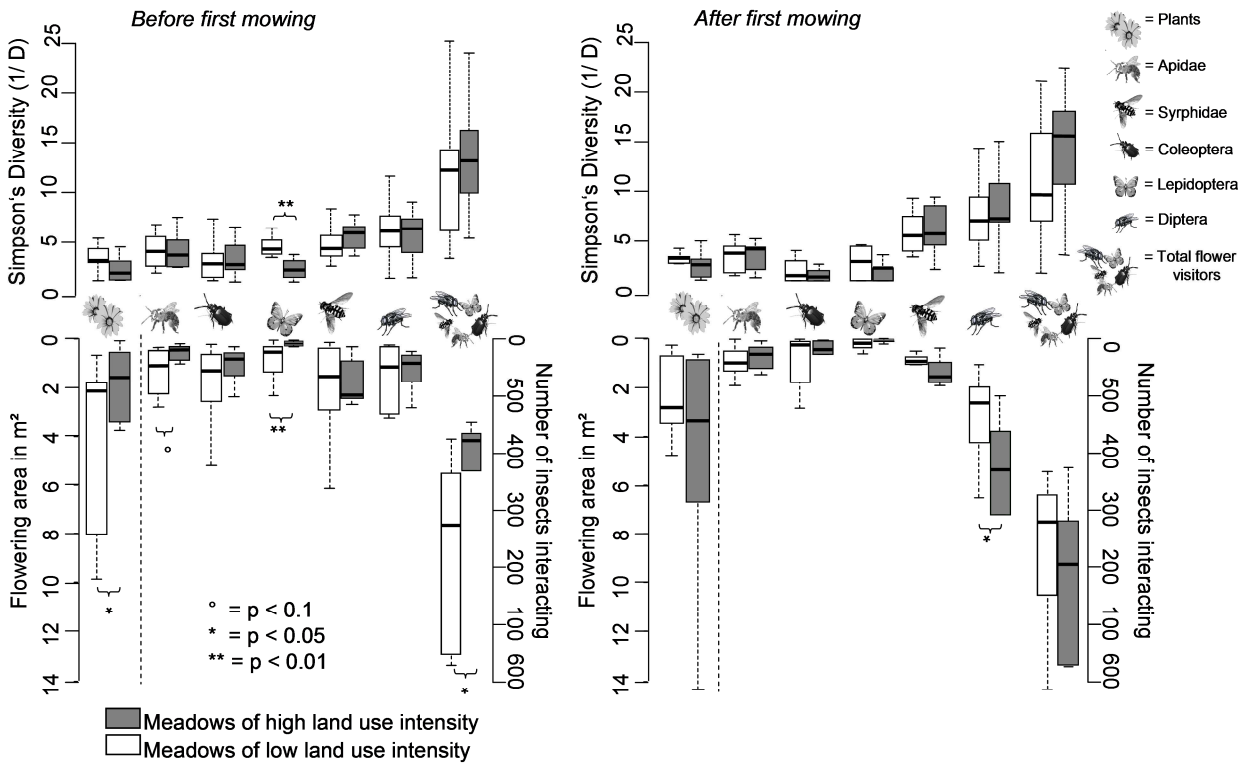

Figure 3: Comparison of flowering area, the number of interacting individuals and Simpson's reciprocal diversity index ($1/\sum p_i^2$) for plants and flower visitors in at low and at high intensity used meadows. Box whisker plots show median, quartiles and range.

Fifty-two butterfly species, 47 beetle species, 67 syrphid species, and 237 other dipteran species were recorded. Bees comprised 54 species, including only five pollen specialists (oligolectic bees). Species richness of butterflies ($t = 3.45$, $p < 0.01$, N = 10 simultaneously sampled plot pairs) and bees ($t = 2.83$, $p < 0.1$) was higher on low-IM before mowing. Butterflies also showed a significantly higher diversity on low-IM before mowing, whereas diversity of other flower-visitors was not consistently affected by land-use intensity (Figure 3).

We recorded more flower visits per plot on low-IM than on high-IM ones before mowing (Figure 3). This was also true for butterflies alone. On the other hand, dipterans were significantly more common in high-IM where the proportion of butterflies was significantly lower (Figure 3, Table 2).

Table 2: Comparison of the proportions of several important flower visitor groups between meadows of low (low-IM) and high (high-IM) land-use intensity (paired t-test)

	Low-IM	High-IM	t-test	
	Mean proportion (%) ± SD		*t*	*p*
Apidae	24.0 ± 17.7	15.0 ± 10.9	1.3	0.226
Coleoptera	16.8 ± 19.6	12.4 ± 11.2	0.5	0.599
Lepidoptera	7.9 ± 9.9	1.9 ± 1.9	2.8	0.012
Syrphidae	15.9 ± 11.0	25.4 ± 20.2	-3.4	0.003
Diptera	30.7 ± 24.4	40.5 ± 21.7	-2.2	0.040
Others	4.9 ± 4.0	4.9 ± 2.8	0.6	0.582

The level of network specialization H_2' was relatively similar for all flower-visitor networks recorded. Its mean value of 0.57 (SD = ± 0.11) was typical for many other flower-visitor networks (Blüthgen et al. 2007). Thus, most networks were highly structured, deviating significantly from random associations. The level of species specialization d_i' was highest for bees, followed by beetles and butterflies, and lowest for syrphids and other dipterans (weighted means across species in each network). Differences were significant between flower visitor groups but not between management types (Figure 4, Table 3).

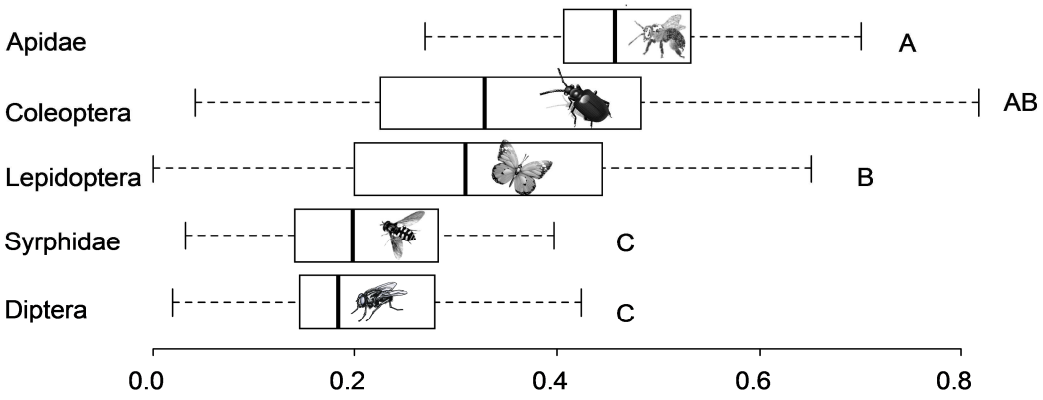

Figure 4: Comparison of individual specialization (*d'*) between different flower visitor groups. Different letters indicate significant differences according to Tukey's post-hoc test. For main effect in ANOVA, see Table 3.

Table 3: Results from repeated measures ANOVA comparing individual specialization (weighted means per flower visitor group and plot) between land-use types (Land use, as repeated measure), flower visitor groups (Taxa), and time before or after mowing (Season).

	SS	*df*	*F*	*p*
Land use	0.04	1	1.65	0.20
Taxa	1.90	4	18.95	< 0.0001
Season	0.00	1	0.03	0.86
Land use × Season	0.00	1	0.03	0.86
Taxa × Season	0.16	4	1.60	0.18
Land use × Taxa	0.12	4	1.32	0.27
Land use × Taxa × Season	0.04	4	0.41	0.80
Error	2.08	83		

2.4 Discussion

Floral and faunal diversity as well as species composition of grasslands partly mirror their management regime (Fenner and Palmer 1998). Our results show that even only gradual differences in management intensity, particularly fertilization of otherwise comparable meadows, strongly affect species composition and diversity of plants and flower visitors. This confirms former studies showing a decreased flower diversity with increased fertilizer application (Mountford et al. 1993).

Increases in resource heterogeneity have often been hypothesized to account for increased pollinator richness (Ghazoul 2006). Especially bee species richness has been shown to increase with plant species richness (Steffan-Dewenter and Tscharntke 2001). In our study, bees and butterflies showed higher species richness in meadows of low land-use intensity, where flower diversity was higher. These differences may also, at least partly, be explained by a higher flower availability (flowering area) found in those meadows before mowing. The number of visitor individuals per meadow varied independently of its total flowering area. Yet, within a meadow, plant species with a larger total flowering area received significantly more visits – indicating that flower abundance plays a role for the distribution of visitors within a site. However, while the

trend in plant species diversity was reversed later in the year, there was no concomitant reversal in species richness and abundance of bees and butterflies in low intensity used meadows. Hence, negative land-use effects on the composition, diversity and abundance of flower visitors are not just triggered by flower abundance but by diversity and species-specific effects like pollinator preferences.

In intensively used meadows we observed more plant-fly interactions than in meadows of low land-use intensity. This may reflect differences in plant species composition: intensively used meadows offered a higher abundance of easily exploitable flowers (Apiaceae, Asteraceae) readily visited by many fly species, particularly later in the season. Flowers with exposed nectar are usually exploited by a wide range of short- and long-tongued insects, resulting in generalized pollination systems (Johnson and Steiner 2000).

Mowing causes temporary declines in diversity and abundance of certain insect taxa and the timing and frequency of mowing markedly alter insect species composition (Bulan and Barrett 1971, Morris 1981, Johst et al. 2006). Direct effects of mowing thus may add to indirect effects by changes in resource supply. Despite this, we observed more flower visitors in late summer (after mowing), especially on meadows of high intensity land use. Here the number of interactions nearly triples compared with the status before mowing (Table 3). Since meadows of high land-use intensity may recover faster after mowing, this effect could mask differences between management types when sampling high-IM and low-IM at the same date. Thereby it seems that management types are not fully comparable after mowing.

Specialized species are often assumed to be more sensitive to disturbance while some generalists may benefit from it (McKinney 1997). This was largely confirmed in our comparison of visitor taxa: dipteran flower visitors were least specialized and showed no consistent changes in species composition related to land-use intensity, while bees and butterflies showed a significantly higher specialization and compositional differences between management types. Species composition of plants and insects is strongly seasonal, which may explain why land-use type only accounts for a small part of the variation in species composition.

The average specialization of beetles was high, but showed strong variation. Some beetle families involve flower specialists, and beetles – depending on their size and

morphology – greatly differ in their ability to access certain flower types (Gullan and Cranston 2005). However, our results within this group are strongly dominated by polyphagous pollen beetles (*Melighetes* cf. *aeneus*, Nitidulidae) which were highly abundant in the samples (72 % of all beetle individuals) and show a variable degree of specialization (mean ± SD, d_i' = 0.5 ± 0.3). Tudor et al. (2004) showed that several butterflies have pronounced flower preferences – often corresponding to species that are currently endangered. Kleijn & Raemakers (2008) demonstrated a relationship between specialization and population declines in bumblebees, using pollen loads from museum specimen collected before 1950: formerly specialized species are currently more likely to be endangered. Furthermore, plant taxa preferred by declining bumble bee species experienced a stronger decline during the 20th century agricultural intensification (Kleijn and Raemakers 2008). Thus, differences in plant species composition together with high specialization may explain the considerable differences in species composition between management types. Furthermore, diversity declines in bees and butterflies suggest that they rely more heavily on their preferred plant species and that these plants are more strongly influenced by management regime than flowers visited by dipterans.

Species diversity and composition of syrphids and other dipterans was not consistently affected by land use in our study, corresponding to their low degree of flower specialization. Our results thus parallel the findings of Biesmeijer et al.(2006), showing that local bee diversity declined much stronger than hoverfly diversity (pre- versus post-1980) attributable to land-use intensification.

We conclude that diversity and abundance of relatively more specialized flower visitors (bees and butterflies) decrease with increasing land-use intensity and that this diversity decline is likely to represent an indirect effect of a lower diversity and altered composition of flowers. Preferred flowers differ between visitor species, resulting in a high complementary specialization in the interactions – a potential reason for the parallel biodiversity decline of consumers and resources. In turn, high complementarity of plant species in regard to their effective pollinators may cause a negative response of plant diversity to pollinator diversity declines.

3. Mutualistic networks and their response to disturbance in relation to diversity and specialization

This chapter has been published as:
Weiner, C.N., Werner, M., Linsenmair, K.-E., Blüthgen, N.: Land-use impacts on plant–pollinator networks: interaction strength and specialization predict pollinator declines. Ecology 95:466–474.

Summary

Land use is known to reduce the diversity of species and complexity of biotic interactions. In theory, interaction networks can be used to predict the sensitivity of species against co-extinction, but this has rarely been applied to real ecosystems facing variable land-use impacts. We investigated plant–pollinator networks on 119 grasslands that varied quantitatively in management regime, yielding 25401 visits by 741 pollinator species on 166 plant species.

Species-specific plant and pollinator responses to land use were significantly predicted by the weighted average land-use response of each species' partners. Moreover, more specialized pollinators were more vulnerable than generalists. Both predictions are based on the relative interaction strengths provided by the observed interaction network. Losses in flower and pollinator diversity were linked, and mutual dependence between plants and pollinators accelerates the observed parallel declines in response to land-use intensification. Our findings confirm that ecological networks help to predict natural community responses to disturbance and possible secondary extinctions.

3.1 Introduction

The ongoing large- and small-scale changes in anthropogenic land use are known to deplete biodiversity (Duraiappah and Naeem 2005). A major goal of biodiversity research is to understand how complex networks of functional interactions between species respond to disturbance and how a gradual loss of biodiversity may affect overall ecosystem function (Loreau et al. 2001, Koh et al. 2004a, Tylianakis et al. 2007).

These questions are of particular concern for the pollination of flowering plants since about 87.5 % of the angiosperms, among them many agricultural crops, depend on

animal pollination (Ollerton et al. 2011). Several studies indicate that agricultural intensification triggers losses in the diversity of plant and pollinator communities due to habitat conversion and fragmentation, fertilization and pesticide use (Cunningham 2000, Burkle and Irwin 2010, Brittain and Potts 2011). Moreover, a high functional diversity of pollinators may sustain a high plant diversity and lead to higher pollination success and seed set of individual plants (Klein et al. 2003, Hoehn et al. 2008). Among-plant competition for limited pollinators may lead to reduction in per capita services to plants in relatively dense or diverse populations (Vamosi et al. 2006). On the other hand, visitors to dense populations are expected to be more flower constant, increasing the chance of pollen transfer between conspecifics (Kunin 1997), and pollination may be more reliable in dense plant populations (Bernhardt et al. 2008). Outcrossing by pollinators is important in the long-term where inbreeding negatively affects population viability and increases local extinction risks (Byers 1995). In turn, high plant diversity is assumed to promote pollinator richness and functional diversity (Kwaiser and Hendrix 2007). Consequently, experiments with manipulated plant species diversity (Ebeling et al. 2008) and comparisons across different meadows (Fründ et al. 2010) demonstrated positive relationships between plant diversity and pollinator diversity and abundance. Additionally, analyses of historic data from Britain and the Netherlands revealed parallel diversity declines in bees and insect pollinated plants (Biesmeijer et al. 2006).

These results lead to the hypothesis that losses in plant and flower-visitor diversity might be causally linked, e.g. a consequence of mutual dependence. Such dependency on certain partners implies that interaction partners are specialized to a considerable degree. To understand land-use effects on interacting species, it is thus crucial to investigate their degree of specialization and the identity of each species' partners. This may allow predictions of how land-use induced changes in species composition would affect natural communities and their functions. Network analysis provides a useful framework for characterizing specialization and predicting vulnerability of resource-consumer relationships or mutualisms to species loss (Montoya et al. 2006).

Some studies suggested that specialist species are prone to disturbance, while generalists benefit from it (McKinney 1997, Aizen et al. 2012, but see Vázquez and Simberloff 2002, Winfree et al. 2007). While some approaches have predicted the vulnerability of complex communities based on simulated extinctions or dynamic

population modeling (Memmott et al. 2007, Pocock et al. 2012), such changes have been rarely tested in real world systems. Methods used in modeling approaches are controversial (Benadi et al. 2012, James et al. 2012), and conflicting conclusions based on empirical data may be partly explained by the fact that specialization metrics differ in their sensitivity to sampling effects (Blüthgen 2010). Since the number of links (observed interaction partners) increases with the number of observations, rarity and specialization are confounded unless corrected by appropriate network metrics (Blüthgen et al. 2007).

In the present study, we focus on specialization and changes in plant-pollinator interactions in grasslands along a gradient of increasing land-use intensity. We hypothesized that (i) land-use intensification triggers a decline in plant diversity and consequently, a plant-mediated decline in the diversity of floral resource consumers. Moreover, we expected (ii) stronger effects of land-use intensification on specialized plant and pollinator species, which are more dependent on their specific partners than generalists are. However, we assumed that (iii) pollinator-mediated declines in plant species are less pronounced than resource-mediated declines of pollinators, since many plant species are not obligatory insect-pollinated and are capable of vegetative reproduction.

3.2 Methods

3.2.1 Study area and land-use intensity

The large-scale Biodiversity Exploratories represent three bioregions in Germany located in the Schorfheide-Chorin (Sch), Hainich-Dün (Hai), and Schwäbische Alb (Alb) (Fischer et al. 2010). Each of the three Exploratories covers a connected area of 422 to ~1300 km² of land and each comprises 50 grassland plots. These plots are situated within a matrix of agricultural land in use and measure 50 m × 50 m each. The minimum distance between the outer edges of two plots is 200 m and each grassland plot is at least 30 m away from the nearest forest edge. A detailed description of all selection criteria for experimental plots is given by Fischer et al. (2010). The plots represent a broad gradient of land-use intensity, ranging from near-natural, protected

sites to intensively fertilized, mown or grazed meadows and pastures (sheep, horses, cattle).

Qualitative categorization of land use such as meadow/pasture or fertilized/unfertilized obscures the variation of intensities within a category, e.g. differences in grazing intensity or fertilizer application. We therefore used a continuous land-use intensity index for grasslands that incorporates the three variables fertilization, mowing and grazing intensity (Blüthgen et al. 2012). For each plot *k*, the land-use intensity L_k is defined as the square root of the sum of these three variables, each of which was standardized by its regional mean (i.e. the mean of each Exploratory):

$$L_k = \sqrt{\frac{G_k}{G_{mean}} + \frac{F_k}{F_{mean}} + \frac{M_k}{M_{mean}}}$$

F_k is the fertilization level (kg nitrogen ha^{-1} $year^{-1}$), M_k the frequency of mowing per year and G_k the livestock density (livestock units $days^{-1}$ ha^{-1} $year^{-1}$) on the site. Due to the standardization by ratios, L_k is dimensionless. We used the mean L_k of the three years 2006 – 2008 for all correlations; although L_k changed only to a small degree between years, this mean value best captures previous and ongoing management which may both effect plants and pollinators. L_k has been shown to predict responses in the vegetation, namely the plants' nitrogen indicator values, nitrogen and phosphorous contents in plant and soil as well as plant diversity (Blüthgen et al. 2012).

3.2.2 Data collection

Between May and August 2008, we investigated plant-flower visitor networks on 119 different experimental grassland plots (Alb: 39; Hai: 39; Sch: 41). 29 plots were investigated repeatedly up to four times (Alb: 15 plots surveyed repeatedly; nine plots two times, three plots three times and three plots four times; Hainich; eight plots surveyed repeatedly; four plots two times, four plots three times; Schorfheide: six plots surveyed repeatedly, five plots two times, one plot three times), resulting in 162 surveys done in total (Alb: 63; Hai: 51; Sch: 48). Each survey covered a time span of six hours between morning and afternoon and an area of 200 × 3 m (length × width) along the edge of the square experimental grassland plot. For this transect, which we walked three times during one survey (three rounds, two hours each), we documented all plant-flower

visitor interactions. We recorded each insect that visited a flower as well as the flower species on which it was observed, but disregarded those insects that were sitting on the outer petals obviously not feeding on pollen or nectar. Specimens that we could not identify in the field were collected and later identified to species level with the help of experts (see Acknowledgements).

To gain independent data on flower abundance, we first counted the number of flowering units per plant species and transect or, in highly abundant species, extrapolated it from a smaller area. One 'flowering unit' was defined as a unit of one (e.g. Ranunculaceae) or more flowers (e.g. Asteraceae) demanding an insect to fly in order to switch to another unit (Dicks et al. 2002). To incorporate differences in flowering area, we assessed flower diversity by multiplying the number of flowering units of a species by its average flowering area in cm^2. In zygomorphic flowers, flowering area was calculated as a rectangle based on flower length and width, while in actinomorphic flowers flowering area was calculated as a circle based on the flower diameter. In umbels we divided the diameter of a flowering unit by two before calculating the flowering area as flowering units are much less compact here than other flowers. This is reasonable, since flower display size is related to pollinator attraction (Grindeland et al. 2005) and also predicted the pollen volume per flower for a subset of the investigated plants for which we have sampled pollen (Pearson, $r = 0.62$, $p = 0.00002$, $N = 40$ plant spp., unpublished data). We obtained data on plant species breeding systems i.e. whether a plant species is potentially self-compatible (autogamous species and species with mixed mating) or not (xenogamous species) from the BiolFlor database (Klotz et al. 2002). Forty-seven plant species are self-incompatible, 12 species show mixed mating, five are autogamous and two species have an apomictic breeding system.

From each survey a single interaction network was compiled and analyzed separately. Use of short-term interaction networks allowed us to record a uniquely high number of network replicates as well as to avoid confounding effects by seasonal variation and non-overlapping phenology. We analyzed all flower visits from insect flower visitors belonging to the orders of Diptera, Hymenoptera, Lepidoptera and Coleoptera. All these visitor taxa are generally known to pollinate and are thus termed "pollinators" in accordance with previous studies, although they may not pollinate each flower on which

they forage. We excluded generally non-pollinating taxa (grasshoppers, spiders), but also Nitidulidae from analysis, as they occurred in particularly high numbers and are easily overlooked and under-sampled in structurally complex flowers, which would bias the analysis.

While in the Hainich and Schorfheide Exploratories we left a minimum interval of 30 days before repeatedly surveying a plot, in the Alb Exploratory regarding 13 repeatedly sampled plots, we had conducted a total of 27 surveys within 30 days (twelve plots were sampled two times, one plot three times within 30 days). To avoid phenologically similar replicates per plot, we calculated mean values from these surveys per plot for each of the variables below before correlating them to land use. This reduced the number of independent replicates on the Alb to 49 instead of 63. The dissimilarity of plant and pollinator assemblages across the remaining repeated surveys from the same plots was high. Repeated surveys from the same plot showed the same or an even higher level of species turnover than surveys from different plots (Appendix Table S1). Mantel tests (Spearman) based on Bray-Curtis distance and 105 permutations showed a strong correlation between plant/insect species composition (based on relative abundances) and sampling date (plants: all $rM \geq 0.15$, all $p \leq 0.0003$, n = 49 Alb, 51 Hai and 48 Sch; insects: all $rM \geq 0.23$, all $p \leq 0.0001$, n = 49 Alb, 51 Hai and 48 Sch). In contrast, the spatial arrangement of the plots did not affect our data (plants: all $rM \leq 0.04$, all $p \geq 0.15$, pollinators: all $rM \leq 0.03$, $p \geq 0.32$). Moreover, land-use intensity neither correlated with sampling date nor spatial distance in any exploratory (all $rM \leq 0.03$, all $p \geq 0.25$). Therefore, despite pronounced temporal variation, we consider our analyses of land-use effects unbiased by spatial and temporal effects.

3.2.3 Statistical analysis

Hitherto most studies have investigated specialization and predicted possible consequences for co-extinctions based on qualitative metrics, i.e. the number of links of each species (“species degree”). Moreover, pooled data over longer temporal or spatial scales were used (e.g. Memmott et al. 2007). Such metrics are prone to variation in sampling effort (Vázquez et al. 2009) and disregard differences in the proportional distribution of species. Species with few observations inevitably have few links, hence specialization of many rare species is severely overestimated due to several undetected

links. This bias has been demonstrated for pollinators when other sources of information of flower use were employed (Dorado et al. 2009). Pooling data over large areas or over long time periods also produces many zeros due to "forbidden links" produced by spatial or temporal non-overlap, which hampers the interpretation of specialization. Therefore, it is important to carefully define specialization based on quantitative metrics independent of sampling effort and species abundances (Dormann et al. 2009) in order to compare the species' responses to disturbance. We thus calculated complementary specialization of plants and pollinators employing the information-theoretical indices H_2' and d_i' (Blüthgen et al. 2006) for each of our short term networks. H_2' specifies the degree of complementary specialization in the entire network, while d_i' characterizes the specialization of each species *i* as its quantitative non-conformity, e.g. its deviation in flower visitation from the distribution of all pollinators. Both indices vary between 0 and 1, with high values corresponding to more pronounced niche complementarity. While H_2' and d_i' are mathematically independent of the total observation frequency per species and per network, due to the standardization based on marginal totals, other network metrics such as species degree, dependence, connectance and nestedness directly reflect variation in species' total frequencies as well as sampling effort (Blüthgen 2010). This bias is also evident in our dataset, where species degree and generality strongly increased with number of observations, whereas d_i' was unaffected (Appendix Figure S1). H_2' was tested against Patefield's null model, running 10000 randomizations (Blüthgen et al. 2006).

We used the weighted mean d_i' of each species *i* across all networks (weighted by the total interaction records of *i* per plot *k*) as well as a weighted mean d_i' for taxonomic groups of flower visitors, namely bees, other hymenopterans, beetles, butterflies, syrphids, and other dipterans. To provide a weighted mean for such a group in each plot *k*, each species *i* was weighted by its total number of individuals recorded in *k*. We segregated bees from other hymenopterans and syrphids from other dipterans, as both are commonly used bioindicator taxa (Biesmeijer et al. 2006).

Our goal was to distinguish effects of niche properties, e.g. specialization and specific partner identity, on species' responses to land use from the effects of species abundances. We thus also tested species abundances (i.e. total number of individuals observed during flower visits, or total flower area for plants) for land-use effects defined below.

For each pollinator species *i* we identified their general response to land-use intensity (r_i). To quantify the sign and magnitude of r_i, we used a Spearman correlation coefficient (labeled as r_S in the results) between the relative abundance of species *i* per plot *k* (per cent of total individuals) and land-use intensity L_k across all plots, including cases where *i* was absent. The same method was applied to quantify the response of each plant species *j* (replace *i* by *j* above, see Figure 5 and Appendix Figure S2).

In addition to the degree of specialization of a species, the identity of its partners may be important. The land-use response of an animal may be determined by the land-use response of its associated plant species, weighted by the plant's relative importance for its partner (interaction frequency) provided in the network. Each plant species *j* of *J* total plant species can be described by its land-use response r_j. The average land-use response of all the food plants frequented by pollinator species *i* (E_i), weighted by the number of interactions a_{ij} between *i* and *j*, is then

$$E_i = \sum_{j=1}^{J} \left(r_j \cdot a_{ij} \right) \Big/ \sum_{j=1}^{J} a_{ij} .$$

Inversely, the average land-use responses of all the pollinator species *i* visiting a plant species *j* is

$$E_j = \sum_{i=1}^{I} \left(r_i \cdot a_{ij} \right) \Big/ \sum_{i=1}^{I} a_{ij} .$$

If the partner identities and interaction strengths of interactions in a network determine the average land-use response of species in a community, we expect a positive correlation between actual species responses and the average responses of their specific partners. Hence, there should be a positive relation $r_i \sim E_i$ across all *I* flower visitors if plants determine the responses of visitors, and $r_j \sim E_j$ across all *J* plants, if pollinators determine the responses of plants. We tested the determinants of those responses r_i and r_j using ANCOVA (type II SS) including the three predictors E_i, d_i' (both continuous) and pollinator group (categorical) for pollinators and E_j, d_j' (both continuous) and breeding system (categorical) for plants. Alternatively to data from our flower surveys, we used binominal vegetation survey data collected on 4 × 4 m quadrats per plot (Blüthgen et al. 2012) to calculate logistic regressions (see Appendix Figure S1b) and used the odds instead of Spearman to calculate r_j and E_i. The alternative approach yielded the same overall results (Figure S2). All statistics were conducted in R 2.15.1 (R Development Core Team 2012).

3.3 Results

Our networks document 25401 interactions between 166 plant species and 741 pollinator species. We identified 115 bee species, including 25 pollen specialists (oligolectic bees), 48 other hymenopterans, 50 butterflies, 104 beetles, 103 syrphids and 321 other dipteran species. A full list of species is provided in the Appendix (Table S2 and S3).

Plant responses: plant species richness (Spearman rank, $r_S = -0.22$ $p = 0.007$, $N = 148$ networks) and Shannon diversity ($r_S = -0.21$ $p = 0.01$) declined with increasing land-use intensity. The average land-use response of a plant species (r_j) was predicted by the weighted response of its pollinator species (E_j), but differed neither with plant specialization nor between self-compatible and self-incompatible plants (Table 4a). Yet, average specialization in plants was very high (mean d_i' ± SD: 0.55 ± 0.22).

Moreover, plant responses to land-use intensity were related to their relative abundance: rare plants (in terms of their proportional coverage of floral area) showed a stronger decline with increasing land use than more abundant ones ($r = 0.22$, $p = 0.005$).

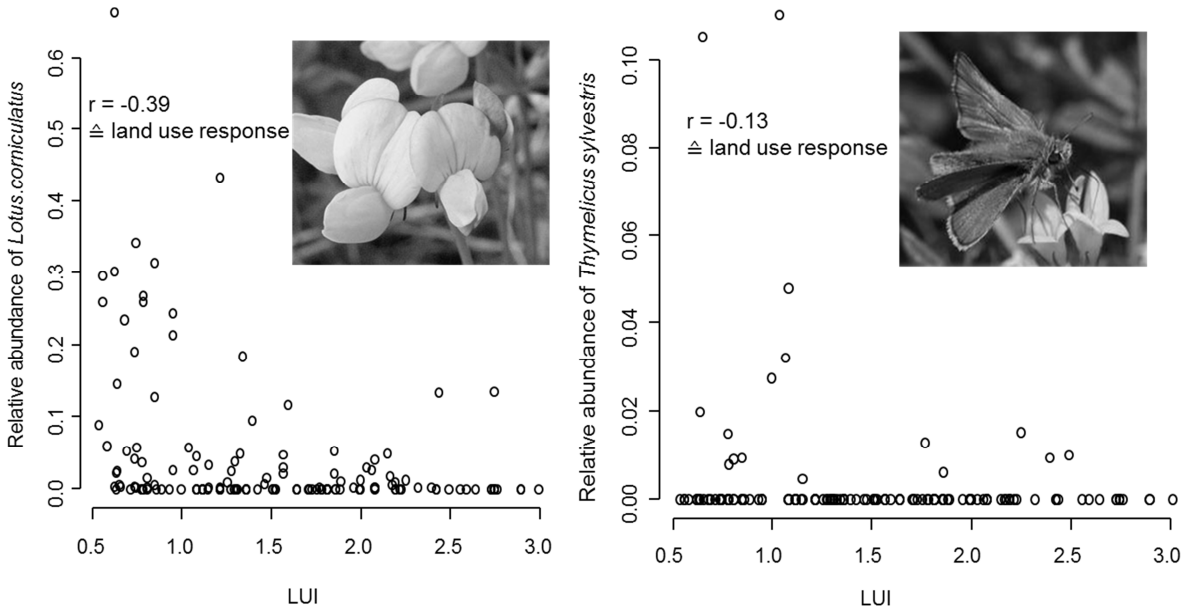

Figure 5: Land-use response (r_s) of (a) *Lotus corniculatus* in terms of relative flower cover and (b) one of its visitors *Thymelicus sylvestris* in terms of relative abundance. In theory, the land-use response of a pollinator may be predicted by the land-use response of its food plants, if land-use affects pollinators mainly indirectly via changes in food resources.

Table 4: (a) Statistical model to predict species-specific plant responses to land use (r_{plants}) based on the weighted average pollinator response E_j (weighted $r_{pollinators}$), specialization (d_j') and breeding system of each plant species. (b) Model to predict pollinator responses ($r_{pollinators}$) based on weighted average plant responses E_i (weighted r_{plants}), specialization (d_i') and pollinator group identity. Complete model and main factors in univariate models are shown (ANCOVA; Type II SS).

(a)	Complete model			Univariate model		
Effect	df	F	p	df	F	p
E_j	1	19.24	**0.00002**	1	19.75	**0.000016**
d_j'	1	0.49	0.4857	1	0.49	0.48
breeding system	1	0.26	0.6140	1	0.23	0.69
$E_j \times d_j$'	1	1.56	0.2141	-	-	-
E_j × breeding system	1	0.42	0.5178	-	-	-
d_j'× breeding system	1	0.02	0.8817	-	-	-

(b)	Complete model			Univariate model		
Effect	df	F	p	df	F	p
E_i	1	228.28	**<0.00001**	1	265.43	**<0.000001**
d_i'	1	0.00	0.9547	1	13.51	**0.000255**
pollinator group	5	4.08	**0.0012**	5	9.90	**<0.000001**
$E_i \times d_i$'	1	6.79	**0.0093**	-	-	-
E_i × pollinator group	5	3.89	**0.0018**	-	-	-
d_i' × pollinator group	5	1.21	0.3030	-	-	-

Pollinator responses: Neither total pollinator species richness ($r_S = 0.08$, $p = 0.32$, $N = 148$) nor abundance ($r_S = –0.001$, $p = 0.99$) or Shannon diversity ($r_S = 0.14$, $p = 0.07$) was correlated to land-use intensity. Pollinator species composition corresponded to flower composition (Mantel tests based on Bray-Curtis distance, all

$r_M \geq 0.22$, $p \leq 0.0001$). Moreover, responses to land-use intensity were independent of pollinator abundance ($r = 0.035$, $p = 0.34$, $N = 741$ pollinator species; Appendix Figure S1d).

Responses of pollinators to land use (r_i) strongly depend on their association with specific flowers, i.e. the weighted mean responses of their plant species visited (E_i) (Table 4b). Pollinator specialization (d_i') was a significant predictor of r_i if treated as the sole variable, but not in the mixed model, where it significantly interacted with E_i (Table 4b). Moreover, pollinator group identity had a significant influence on pollinator response (r_i) to land use (Table 4). Regarding the interaction term between d_i' and E_i, land-use responses of highly ($d_i' \geq 0.6$, $n = 38$) and intermediately specialized pollinators ($0.2 \leq d_i' < 0.6$, $n = 261$) were more strongly driven by the responses of their preferred plants than in more generalized pollinators ($d_i' < 0.2$, $n = 442$, Figure 6). However, plant species that support unspecialized and intermediately specialized pollinators were more vulnerable to land use than plant species supporting highly specialized pollinators: there was a negative relationship between pollinator specialization and the land-use response of their resources ($r_S = -0.26$, $p < 0.0001$, $n = 741$). For highly specialized pollinators the trend had an opposite direction (Appendix Figure S4).

Regarding the interaction term between pollinator group identity and E_i, bees and other hymenopterans, butterflies, beetles and flies excl. syrphids strongly reflected the land-use response of the plant species they visited in their own relative abundances. In contrast, syrphids seemed to respond to land-use changes independently from the responses displayed by the plants they visited (Table 4, Appendix Figure S5).

With increasing land-use intensity the proportion of syrphid species increased, whereas the proportion of butterfly and hymenopteran species excl. bees decreased. The proportion of bee, beetle and dipteran species excl. syrphids did not show significant trends across the Exploratories (Table 5), although bees significantly declined and dipterans significantly increased with land-use intensity in the Alb ($r_S = –0.38$, $p = 0.007$ and $r_S = 0.47$, $p < 0.001$, respectively).

Table 5: Land-use responses (changes in species richness with increasing land-use intensity, Spearman's r_S) and flower specialization (d_i') of six pollinator groups.

Pollinator group	r_S	p	mean d_i'	SD
bees	-0.04	0.64	0.39	± 0.22
other hymenopterans	-0.21	0.01	0.28	± 0.23
butterflies	-0.28	< 0.0005	0.33	± 0.24
beetles	-0.10	0.24	0.27	± 0.21
syrphids	0.21	0.01	0.24	± 0.16
other dipterans	0.09	0.26	0.25	± 0.19

Plant-pollinator networks deviated significantly from random associations and were highly structured (mean network specialization H_2' = 0.63, SD = ± 0.17, N = 148). Most networks were significantly different from Patefield's null model of random interactions ($p < 0.001$ for 130 networks and $p < 0.05$ for additional 9 networks). Network specialization was not consistently related to land-use intensity ($r_S = 0.11$, $p = 0.22$). Species specialization d_i' differed between pollinator groups (Kruskal-Wallis $\chi^2 = 55.50$, $p < 0.0001$). It was strongest for bees and butterflies, intermediate for beetles and hymenopterans and lowest for syrphids and other dipterans (Table 5).

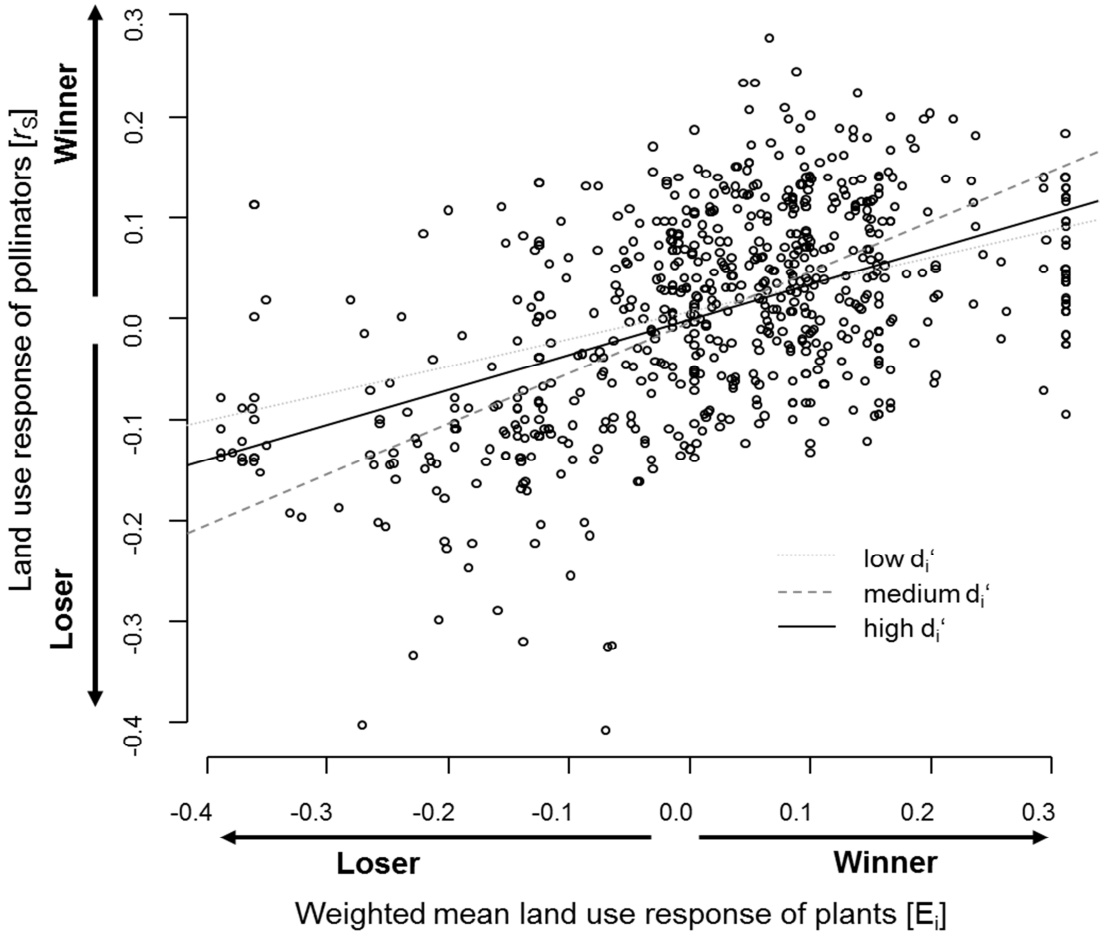

Figure 6: Interaction strengths in quantitative networks predict indirect effects of land-use intensification: Pollinator abundances decrease in response to declines of their most frequently visited plant species. Therefore, for the sensitivity of a species it is not only important *how* specialized it is, but also on *whom* it is specialized. Regression lines are shown for pollinators with low (d_i' < 0.2), intermediate (0.2 ≤ d_i' < 0.6) and high (d_i' ≥ 0.6) degree of specialization.

3.4 Discussion

Our results demonstrate four important land-use effects on plant-pollinator interactions: (1) Land-use intensification primarily triggers losses in flower diversity, which could lead to non-random and resource-mediated declines in certain pollinators. Overall pollinator diversity is not significantly affected by land use, but pollinator composition is. (2) Although responses of the pollinators visiting a plant species may also influence plant abundance, this effect is weaker. (3) Land-use intensification has a disproportionate impact on the abundance of more specialized pollinators, (4) but not on the abundance of specialized plant species.

The linkage between a pollinator's response and the response of the plant species it visits potentiates for specialized pollinators, i.e. specialists on plants that profit from land use are increasing, while those on negatively affected plant species decrease accordingly. A strong dependence of pollinators on a narrow set of plant species is associated with higher co-extinction risk, since these plant species cannot be functionally replaced by others (Praz et al. 2008). Moreover, in communities characterized by low response diversity and low functional redundancy, resilience after disturbance and the ability to buffer environmental changes are reduced (Elmqvist et al. 2003, Laliberte et al. 2013). Negative impacts of specialization may be partly compensated by a higher efficiency of specialists, e.g. specialist bees are very effective in finding flowers, pollen collection and digestion (Strickler 1979, Dobson and Peng 1997), but the general extent of such compensation is unknown.

Our findings are consistent with the hypothesis that pollinator declines are driven by the disappearance of their important host plants, while the reciprocal effects of pollinators on plants are weaker. In this type of mutualism, the composition of plant communities may be relatively robust against losses of particular pollinators, at least in the short term covered by our study (Kalisz et al. 2004). Most grassland plants involved in our study are self-compatible and/or have vegetative reproduction modes (Klotz et al. 2002) and thus our surveys may not be suitable to detect effects of reduced genetic diversity in plant populations that may occur with pollinator losses. While plant reproductive fitness and outcrossing may be at risk over longer time spans, the immediate effects on the fitness and/or local distribution of pollinator communities may be more severe when their important floral resources become unavailable (Biesmeijer et al. 2006, Goulson et al. 2008). The asymmetry in local extinction risks may be increased by the fact that pollinators typically provide several times more species per network than plants and thus a larger buffer (Blüthgen et al. 2007), also mirrored in our data (flowering plants: 8.4 ± 4.4 species, visiting pollinators: 31.9 ± 15.2 species, n = 148 networks). The mutual specialization and thus dependence between pollinator and plant species may lead to parallel regional declines in historical comparisons (Biesmeijer et al. 2006, Fründ et al. 2010). Correspondingly, the more generalized syrphids suffered less from regional extinctions (and often even gained a higher diversity in some regions) in recent decades than the more specialized bee species (Biesmeijer et al. 2006, Jauker et al.

2009). These trends are also reflected in their responses to land use in our study. Land-use intensification not only causes a loss in plant diversity, but also translates into pronounced changes in pollinator communities. The changes in pollinator composition – the dominance of flies and declines in many other taxa – correspond to a biotic homogenization (Filippi-Codaccioni et al. 2010) on high intensity grasslands. Species richness and abundance of syrphids was also positively influenced by land-use intensification in other studies (Biesmeijer et al. 2006, Ebeling et al. 2008, Jauker et al. 2009), whereas bee diversity and abundance declined (Biesmeijer et al. 2006, Le Féon et al. 2010). This process is easily overlooked when focusing on total biodiversity only. Land-use intensification reduces taxonomic breadth and functional diversity, which could conversely affect plant reproductive success, species richness and functional diversity (Klein et al. 2003, Hoehn et al. 2008). In a South African ecosystem, Pauw (2007) showed that among seven species of orchids, those that were more specialized suffered severely from the loss of the single pollinator species.

Dipteran pollinators showed the lowest specialization for plant species, whereas bees, other hymenopterans, butterflies and beetles were more specialized (see also Weiner et al. 2011), confirming that specialization represents a risk that renders species more vulnerable to co-extinction (McKinney 1997, Vázquez and Simberloff 2002, Winfree et al. 2007, Aizen et al. 2012, Pocock et al. 2012). Correspondingly, investigations on butterflies (Tudor et al. 2004), beetles (Kotze and O´Hara 2003) and bumblebees (Kleijn and Raemakers 2008) demonstrated that many specialized species are of conservation concern and have undergone a considerable decline in the last decades.

In addition to indirect effects via flower composition and availability, land use may affect pollinators directly e.g. via disruption of life cycles (Johst et al. 2006) or supply of appropriate nesting resources (Potts et al. 2005) or larval habitats. Many bees and beetles show preferences for certain environmental conditions, larval or nesting sites, and their abundance depends on certain habitats and landscape structures (Gathmann and Tscharntke 2002). On the other hand, generalized flower visitors like most syrphids and other dipterans are not restricted to certain landscape structures and may profit from diverse larval habitats (Jauker et al. 2009). Over longer time spans, such direct land-use effects on pollinators may transform into pollinator-mediated effects on plant

communities. However, in the short term covered by our study land-use effects on plants and plant-mediated effects on pollinators played a greater role than vice versa.

Our findings emphasize how systems based on mutualism may undergo severe transformation due to land-use intensification. Agricultural management is a major factor driving the change of floral and faunal richness in anthropogenic landscapes. Network analyses, particularly the degree of complementary specialization and the quantitative interaction strength, may provide important tools to predict how different species respond to disturbance and biodiversity changes in real communities.

Appendix: Specialization metrics, land-use responses and species lists

Alternative specialization metrics

In the main text, we focused on the information-theoretic specialization metrics H_2' and d_i' developed earlier (Blüthgen et al. 2006). These metrics control for the effects of variable number of observations per species and per network by a standardization based on fixed marginal totals. The standardization constrains the observed entropy H_2 and Kullback-Leibler distance d_i into a continuous index between 0 and 1, ranging from completely random associations (maximum possible H_2, minimum d_i) to the maximum possible specialization (minimum H_2, maximum d_i). Whereas d_i characterizes the specialization for each species, H_2' reflects the overall degree of specialization for the entire network and is related to the weighted mean d_i across all species (Blüthgen et al. 2007). Because d_i' of a species *i* depends on the distribution of all other species (marginal totals), it increases with the exclusiveness of the interaction partners with which *i* interacts, hence d_i' and H_2' describe the degree of *complementary* specialization (Blüthgen 2010). A straightforward alternative to quantify specialization would have been to use a rarefied diversity index used in many diversity studies or in a recent plant-pollinator network (Chacoff et al. 2012), but we did not follow this approach due to the low number of observations for a large proportion of species. Many rare pollinator species were observed just once (28% singletons) or very few times (52% had fewer than 5 individuals in total). For a number of rare plant species, only one or few visits were recorded (14% with only one visit, 27% with <5 visits). Hence, rarefaction to a meaningful threshold would dramatically reduce the dataset in our study and in many other studies, leading to an undesirable underrepresentation of rare species and overrepresentation of common species in the analyses.

Other commonly used specialization metrics are strongly confounded by the total number of observations per species, i.e. specialization decreases with frequency and is highest for species with a single observation (Blüthgen 2010). This bias is evident for the commonly used metrics "species degree" and "generality". Species degree describes the number of links of a species *i* (i.e. the *richness* of its interaction partners), and generality of species *i* is the frequency-weighted *diversity* of its interaction partners. (Usually, generality is defined as the average across all species rather than for single species, e.g. Tylianakis et al. 2007). We calculated "weighted generality" for each

species as the exponential transformation of the Shannon diversity index, e^H. We pooled all our single-day networks from different regions into a single network to obtain species degree and e^H. As expected, both indices increase strongly with the number of observations per species (Figure S1a, b). Only the standardized d_i is largely independent of the number of observations (Figure S1c); species with few observations show a stronger variation but no trend in the mean (see also Blüthgen et al. 2006). Hence, we can test specialization based on d_i' separately from abundance unlike the other specialization metrics (see main text). The effect of pollinator abundance on their land-use response is shown in Figure S1d. The relationship between pollinator specialization d_i' and response to land use was not confirmed when the uncorrected species degree or e^H were used ($p \geq 0.24$). Surprisingly, the level of generalization expressed by species degree or e^H was even positively related to the corrected metric d_i' (species degree ~ d_i' and e^H ~ d_i': Spearman $r_S = 0.36$, $p < 0.001$). For plants, total number of visits also strongly predicted each species' degree ($r^2 = 0.96$) and e^H ($r^2 = 0.81$), whereas d_i was again largely independent of the total visitation ($r^2 = 0.05$). Unlike d_i, species degree significantly predicted the plant's responses to land use ($r = 0.19$, p = 0.01), and e^H showed a similar trend ($r = 0.14$, p = 0.08), but their effect is not independent of the stronger abundance effect shown in the main text, considering the correlation with total number of visits. Species degree and e^H were again slightly positively related to d_i' (species degree ~ d_i': Spearman $r_S = 0.22$, $p = 0.004$; e^H ~ d_i': $r_S = 0.17$, $p = 0.03$).

Species turnover within and across plots

Due to a pronounced seasonality of flowers and occasional visits of mobile pollinators, repeated surveys from the same plots after at least 30 days often yielded highly different communities, which we consequently used as independent networks in our analyses. The average dissimilarity between repeated surveys was as high or even higher than the dissimilarity between plots. Table S1 summarizes the Bray-Curtis distances of the pollinator and plant communities (based on proportional abundance data) across surveys within the same plot versus across plots.

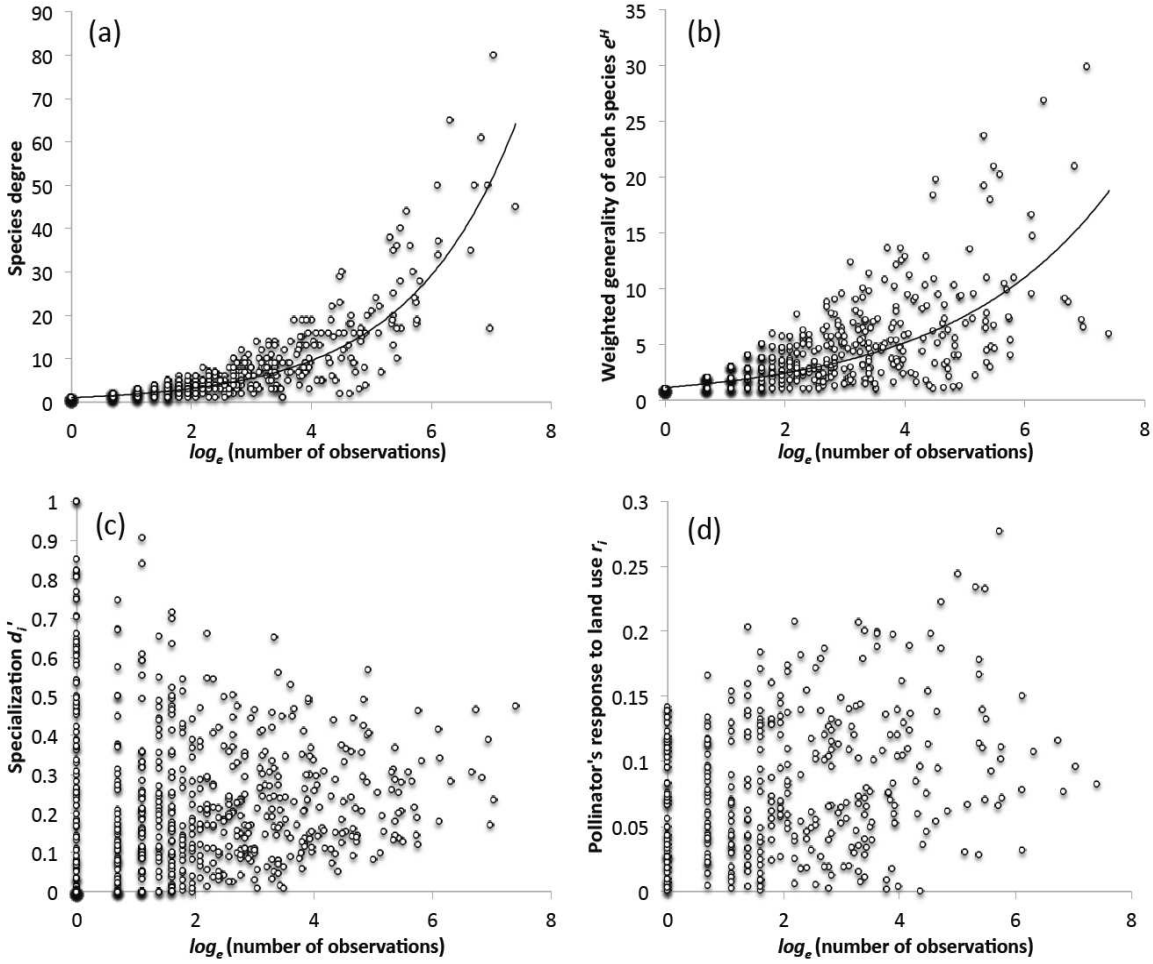

Figure S1: (a–c) Total number of observations of each pollinator species (n = 741 spp.) strongly predicts its "specialization" in terms of species degree (r^2 = 0.83, exponential regression) or generality (r^2 = 0.64), but not d_i (r^2 = 0.02, linear regression). Observation totals were log_e transformed. (d) Rare species did not show stronger responses to land use than common ones (see main text).

Table S1: Mean (±SD) Bray-Curtis distances of plant and pollinator communities between repeated surveys of the same plot and between different plots in the three Exploratories. Seasonal variation within plots was similar or even higher than variation across plots.

	Alb	Hainich	Schorfheide
Flower communities			
Within plots	0.83 (±0.12)	0.95 (±0.08)	0.86 (±0.19)
Across plots	0.83 (±0.16)	0.89 (±0.14)	0.86 (±0.21)
Pollinator communities			
Within plots	0.87 (±0.09)	0.91 (±0.07)	0.93 (±0.05)
Across plots	0.83 (±0.12)	0.90 (±0.11)	0.91 (±0.09)

Land-use responses

Land-use responses of plants and pollinators were defined as the changes in species' abundances across the land-use gradient. For example, the flower cover of *Lotus corniculatus* (Fabaceae) declined strongly with increasing land-use intensity (Figure 5 and S2a). This was also evident from vegetative surveys, where the presence/absence of plant species was recorded in 4 × 4 m quadrates (Figure S2b).

Across all 741 pollinator species, we showed in the main document (Figure 6) that their response to land use was strongly determined by the responses of their preferred plants, based on the momentary flower cover. Correspondingly, the same effect was obtained when plant responses were evaluated based on vegetative surveys, with $r = 0.49$, $p < 0.0001$ (Figure S3). Therefore, the coupling of pollinator and plant responses was not simply due to the momentary availability of flowers to the visitors, but also supported by an independent evaluation of the plants' responses.

While we found an overall negative relationship between pollinator specialization and the land-use response of their resources, a more detailed look revealed that plants visited by highly specialized pollinators seem to be less vulnerable to land use than plant species that support unspecialized and intermediately specialized pollinators (Figure S4).

In contrast to all other pollinator-groups, land-use responses of syrphids were not related to the land-use response of the plant species they visited (Figure S5). The species names, land-use responses and other data for all pollinator and plant species are provided in Table S1 and S2, respectively.

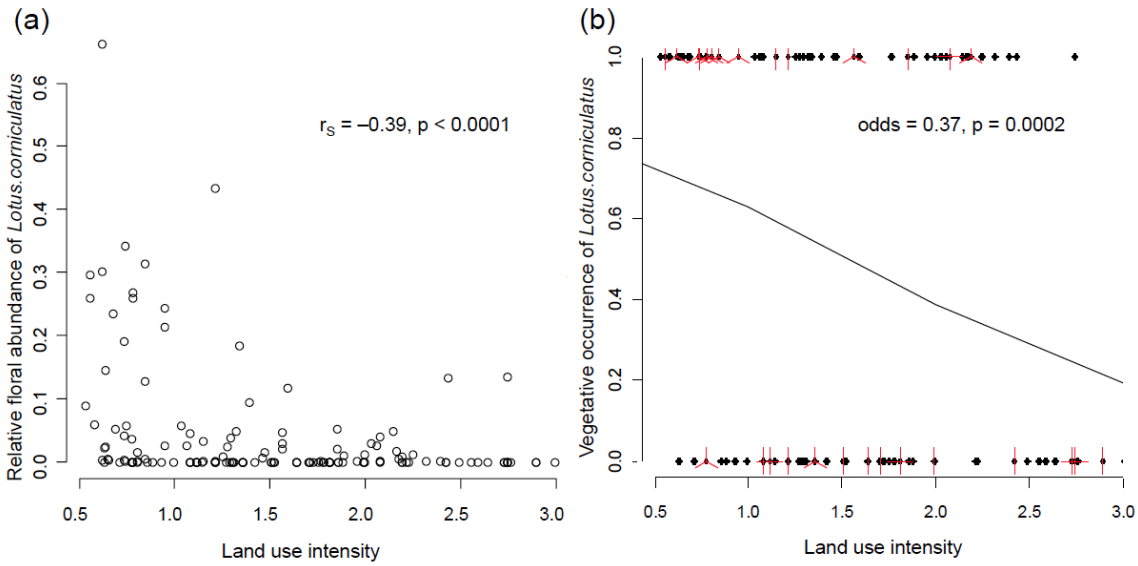

Figure S2: Land-use response of *Lotus corniculatus* in terms of (a) flower cover (Spearman rank) and (b) presence/absence (logistic regression).

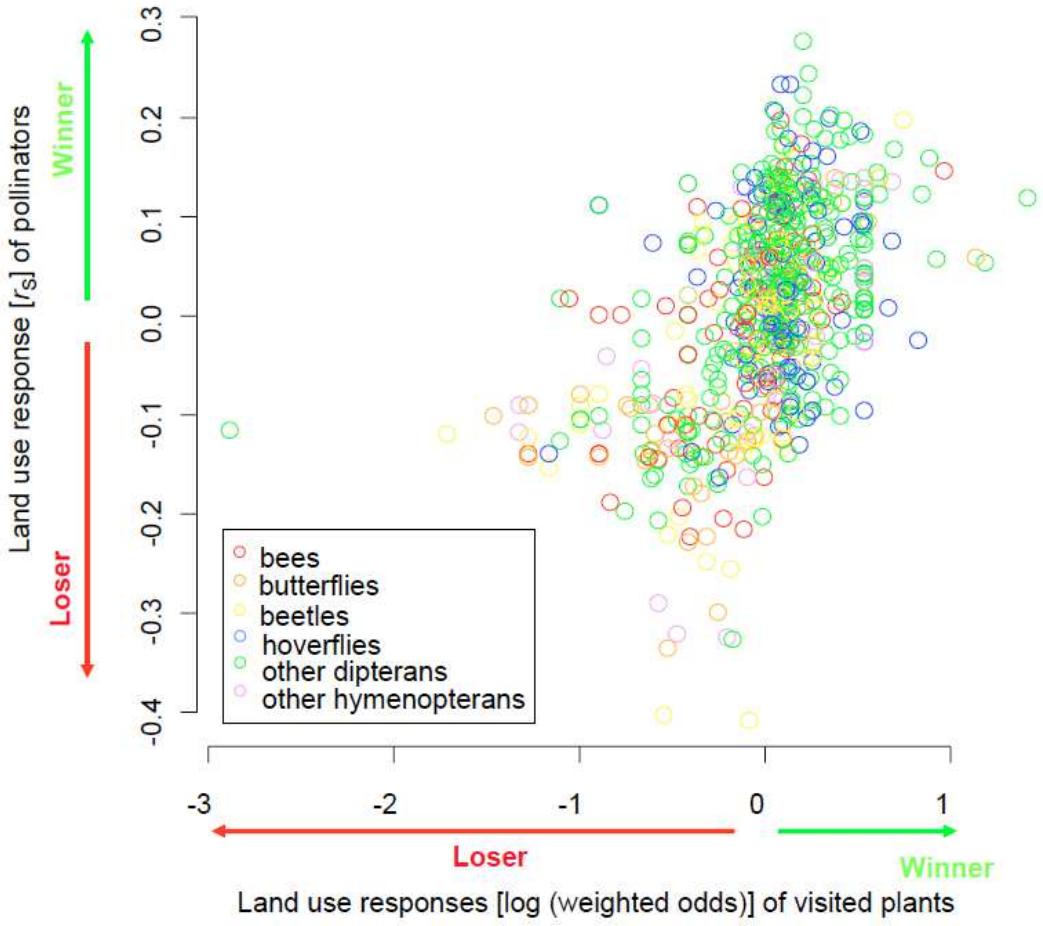

Figure S3: Plant and pollinator responses were coupled: pollinator abundances decreased in response to declines of their most frequently visited plant species as an effect of land-use intensity. Here we used the odds (log transformed) of the logistic regression describing the plants' occurrences to quantify their land-use responses (see Figure S1b).

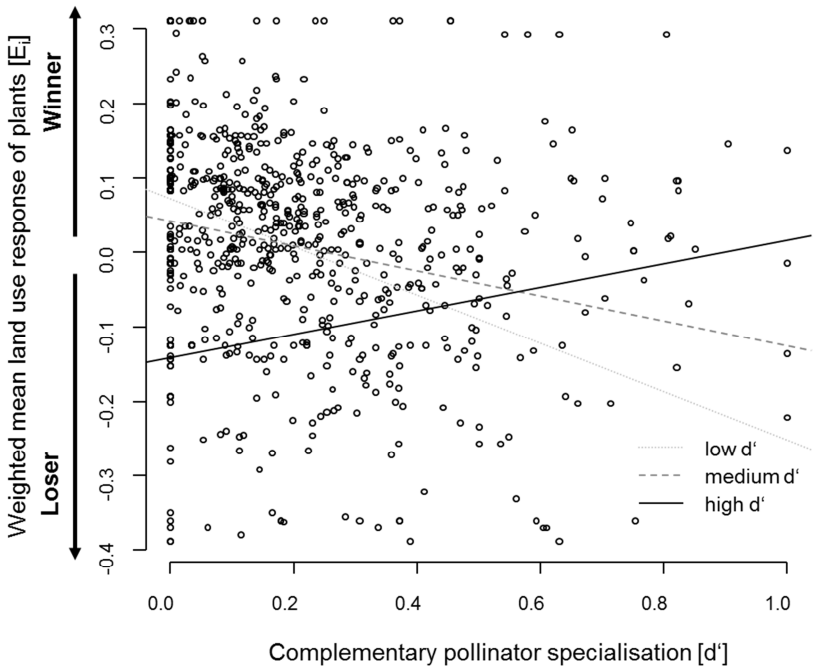

Figure S4: Relationship between plant specialization of pollinator species and the land-use response of their food resources.

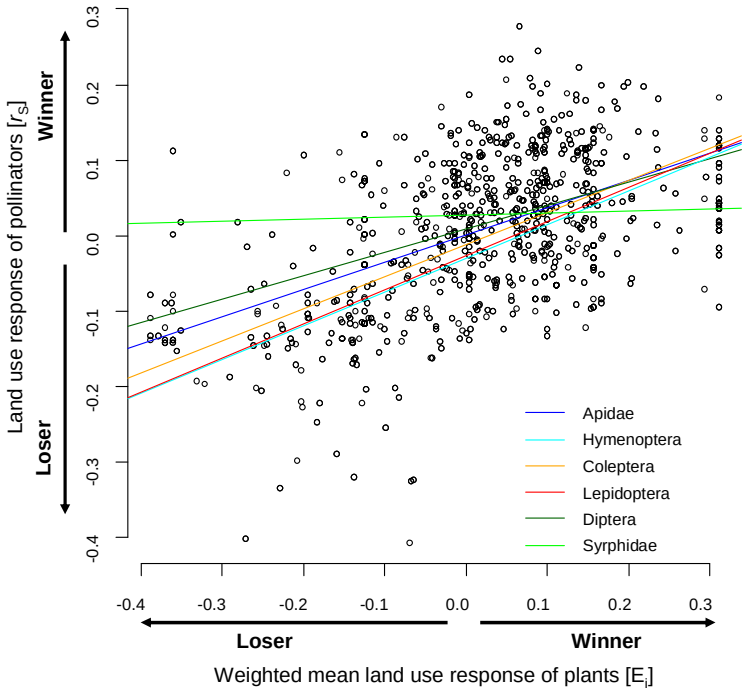

Figure S5: Plant and pollinator responses are coupled for all pollinator groups except of syrphids. Syrphid abundances do not reflect land-use responses of their most frequently visited plant species.

Table S2: Abundance, number of flower species visited, specialization (d_i') and land-use responses (mean r_S) of 741 pollinator species.

Order	Family	Species	Number of individuals	Number of flower species visited	Weighted mean d_i'	Mean land-use response (r_S)
Coleoptera	Apionidae	*Ischnopterapion virens*	1	1	0.00	0.0270
Coleoptera	Apionidae	*Protapion apricans*	1	1	0.39	-0.0840
Coleoptera	Apionidae	*Protapion assimile*	1	1	0.05	0.1390
Coleoptera	Apionidae	*Protapion fulvipes*	2	1	0.11	0.0689
Coleoptera	Apionidae	*Protapion nigritarse*	1	1	1.00	0.0830
Coleoptera	Apionidae	*Protapion trifolii*	1	1	0.00	0.0145
Coleoptera	Apionidae	*Pseudoperapion brevirostre*	1	1	0.66	0.0097
Coleoptera	Bostrichidae	*Bostrichus capucinus*	1	1	0.00	-0.0898
Coleoptera	Buprestidae	*Agrilus biguttatus*	1	1	0.06	-0.1419
Coleoptera	Buprestidae	*Anthaxia quadripunctata*	3	2	0.16	-0.0148
Coleoptera	Cantharidae	*Cantharis figurata*	6	3	0.28	0.1605
Coleoptera	Cantharidae	*Cantharis flavilabris*	27	8	0.33	0.0151
Coleoptera	Cantharidae	*Cantharis fusca*	177	7	0.15	0.0663
Coleoptera	Cantharidae	*Cantharis livida*	9	4	0.01	0.0063
Coleoptera	Cantharidae	*Cantharis pellucida*	1	1	0.81	0.0145
Coleoptera	Cantharidae	*Rhagonycha fulva*	94	12	0.15	0.1979
Coleoptera	Cantharidae	*Rhagonycha nigriventris*	45	4	0.06	0.0762
Coleoptera	Carabidae	*Amara familiaris*	1	1	0.54	0.0492
Coleoptera	Carabidae	*Amara nitida*	2	1	0.38	-0.0145
Coleoptera	Cerambycidae	*Alosterna tabacicolor*	1	1	0.00	0.1187
Coleoptera	Cerambycidae	*Anastrangalia sanguinolenta*	2	2	0.21	0.1133
Coleoptera	Cerambycidae	*Dinoptera collaris*	1	1	0.00	0.1187
Coleoptera	Cerambycidae	*Gaurotes virginea*	2	2	0.27	0.1338
Coleoptera	Cerambycidae	*Paracorymbia maculicornis*	5	3	0.35	0.0089
Coleoptera	Cerambycidae	*Pseudovadonia livida*	135	16	0.40	-0.0616
Coleoptera	Cerambycidae	*Rutpela maculata*	5	4	0.20	0.1085
Coleoptera	Cerambycidae	*Stenurella bifasciata*	47	6	0.26	-0.2473
Coleoptera	Cerambycidae	*Stenurella melanura*	139	20	0.41	-0.0971
Coleoptera	Cerambycidae	*Stictoleptura rubra*	1	1	0.00	0.0222
Coleoptera	Cetoniidae	*Cetonia cf. aurata*	1	1	0.45	0.1390
Coleoptera	Chrysomelidae	*Bruchidius seminarius*	1	1	0.82	0.1101
Coleoptera	Chrysomelidae	*Bruchus atomarius*	1	1	1.00	-0.1187
Coleoptera	Chrysomelidae	*Cassida denticollis*	2	1	0.27	0.0956
Coleoptera	Chrysomelidae	*Cassida nebulosa*	1	1	0.00	-0.0290
Coleoptera	Chrysomelidae	*Chaetocnema concinna*	1	1	0.75	-0.1284
Coleoptera	Chrysomelidae	*Clytra laeviuscula*	1	1	0.30	-0.1245
Coleoptera	Chrysomelidae	*Cryptocephalus aureolus*	103	18	0.36	-0.4012
Coleoptera	Chrysomelidae	*Cryptocephalus hypochaeridis*	127	15	0.49	-0.4061
Coleoptera	Chrysomelidae	*Cryptocephalus pusillus*	1	1	0.00	0.0270
Coleoptera	Chrysomelidae	*Cryptocephalus vittatus*	14	8	0.37	-0.2022
Coleoptera	Chrysomelidae	*Labidostomis tridentata*	3	1	0.91	-0.1226
Coleoptera	Chrysomelidae	*Neocrepidodera ferruginea*	1	1	0.00	-0.0840
Coleoptera	Chrysomelidae	*Neocrepidodera transversa*	4	2	0.42	-0.0463
Coleoptera	Chrysomelidae	*Phyllotreta nemorum*	1	1	0.00	-0.0125
Coleoptera	Chrysomelidae	*Phyllotreta vittula*	1	1	0.03	-0.1168
Coleoptera	Chrysomelidae	*Psylliodes chrysocephalus*	1	1	0.26	0.0097
Coleoptera	Chrysomelidae	*Sermylassa halensis*	3	3	0.49	-0.1211

Coleoptera	Chrysomelidae	*Sphaeroderma testaceum*	1	1	0.48	-0.1043
Coleoptera	Cleridae	*Trichodes alvearius*	1	1	0.60	-0.1226
Coleoptera	Cleridae	*Trichodes apiarius*	4	1	0.32	0.0328
Coleoptera	Coccinellidae	*Adalia bipunctata*	1	1	0.00	0.0029
Coleoptera	Coccinellidae	*Coccinella septempunctata*	73	16	0.24	0.0850
Coleoptera	Coccinellidae	*Coccinula quatuordecimpustulata*	4	3	0.04	0.0546
Coleoptera	Coccinellidae	*Harmonia axyridis*	1	1	0.08	-0.1323
Coleoptera	Coccinellidae	*Hippodamia notata*	1	1	0.00	0.0695
Coleoptera	Coccinellidae	*Hippodamia variegata*	78	6	0.10	0.0965
Coleoptera	Coccinellidae	*Oenopia conglobata*	1	1	0.82	-0.0338
Coleoptera	Coccinellidae	*Propylea quatuordecimpunctata*	7	6	0.18	0.1297
Coleoptera	Coccinellidae	*Tytthaspis sedecimpunctata*	48	8	0.30	0.0173
Coleoptera	Curculionidae	*Anthonomus rubi*	5	3	0.18	-0.1233
Coleoptera	Curculionidae	*Cleopomiarus graminis*	9	4	0.66	-0.2208
Coleoptera	Curculionidae	*Glocianus punctiger*	1	1	0.00	-0.0415
Coleoptera	Curculionidae	*Hypera meles*	2	2	0.5	-0.1081
Coleoptera	Curculionidae	*Hypera rumicis*	1	1	0.00	-0.0290
Coleoptera	Curculionidae	*Larinus turbinatus*	5	2	0.21	0.0200
Coleoptera	Curculionidae	*Miarus campanulae*	3	2	0.84	-0.1014
Coleoptera	Curculionidae	*Phyllobius pyri*	2	1	0.18	0.0608
Coleoptera	Curculionidae	*Phyllobius roboretanus*	1	1	0.00	-0.0782
Coleoptera	Curculionidae	*Sitona lepidus*	1	1	0.00	0.0270
Coleoptera	Curculionidae	*Sitona puncticollis*	1	1	0.27	0.0222
Coleoptera	Curculionidae	*Tychius picirostris*	3	2	0.36	0.0072
Coleoptera	Curculionidae	*Zacladus geranii*	122	3	0.20	-0.0416
Coleoptera	Dasytidae	*Dasytes fusculus*	2	2	0.28	-0.1532
Coleoptera	Dasytidae	*Dasytes niger*	1	1	0.65	0.1390
Coleoptera	Dasytidae	*Dasytes plumbeus*	5	4	0.49	0.1708
Coleoptera	Elateridae	*Agriotes gallicus*	1	1	0.00	-0.1361
Coleoptera	Elateridae	*Agriotes lineatus*	4	1	0.00	0.0859
Coleoptera	Elateridae	*Agriotes sputator*	17	5	0.25	0.0448
Coleoptera	Elateridae	*Agrypnus murinus*	21	6	0.21	-0.0217
Coleoptera	Elateridae	*Athous haemorrhoidalis*	3	2	0.00	0.0027
Coleoptera	Elateridae	*Athous subfuscus*	4	2	0.47	-0.0663
Coleoptera	Elateridae	*Cidnopus pilosus*	4	3	0.49	-0.1091
Coleoptera	Elateridae	*Ctenicera pectinicornis*	1	1	0.00	0.0695
Coleoptera	Elateridae	*Dicronychus cinereus*	2	1	0.00	0.0209
Coleoptera	Elateridae	*Hemicrepidius niger*	17	7	0.29	0.1328
Coleoptera	Elateridae	*Limonius minutus*	8	4	0.16	0.0479
Coleoptera	Elateridae	*Prosternon tessellatum*	10	6	0.27	0.0178
Coleoptera	Elateridae	*Selatosomus aeneus*	1	1	0.64	-0.1091
Coleoptera	Malachiidae	*Malachius bipustulatus*	19	11	0.11	0.0599
Coleoptera	Mordellidae	*Mordella holomelaena*	6	4	0.41	-0.0362
Coleoptera	Mordellidae	*Mordellistena brevicauda*	51	13	0.35	-0.1296
Coleoptera	Oedemeridae	*Chrysanthia geniculata*	2	1	0.00	-0.0048
Coleoptera	Oedemeridae	*Chrysanthia viridissima*	2	2	0.00	-0.1361
Coleoptera	Oedemeridae	*Oedemera femorata*	51	19	0.30	0.0521
Coleoptera	Oedemeridae	*Oedemera flavipes*	3	3	0.33	0.0676
Coleoptera	Oedemeridae	*Oedemera lurida*	160	24	0.25	-0.2539
Coleoptera	Oedemeridae	*Oedemera podagrariae*	9	3	0.22	-0.0332
Coleoptera	Phalacridae	*Olibrus aeneus*	5	2	0.13	0.0935
Coleoptera	Phalacridae	*Olibrus bicolor*	88	2	0.13	0.0459
Coleoptera	Rutelidae	*Hoplia argentea*	8	5	0.26	-0.0637
Coleoptera	Rutelidae	*Phyllopertha horticola*	17	6	0.17	0.0128
Coleoptera	Scraptiidae	*Anaspis frontalis*	6	4	0.42	0.0733

Coleoptera	Staphylinidae	*Tachyporus pusillus*	3	1	0.59	-0.0782
Coleoptera	Tenebrionidae	*Cteniopus flavus*	6	2	0.03	0.0505
Diptera	Agromyzidae	*Liriomyza centaureae*	1	1	0.03	-0.1168
Diptera	Agromyzidae	*Melanagromyza cunctans*	1	1	0.39	-0.1390
Diptera	Agromyzidae	*Napomyza lateralis*	1	1	0.00	0.0048
Diptera	Agromyzidae	*Ophiomyia curvipalpis*	5	1	0.25	-0.1149
Diptera	Agromyzidae	*Ophiomyia nasuta*	26	8	0.31	0.1421
Diptera	Agromyzidae	*Ophiomyia pinguis*	8	6	0.39	0.0753
Diptera	Agromyzidae	*Ophiomyia pulicaria*	3	3	0.10	0.0350
Diptera	Agromyzidae	*Ophiomyia ranunculicaulis*	1	1	0.14	-0.0840
Diptera	Agromyzidae	*Phytomyza albipennis*	12	3	0.50	-0.1043
Diptera	Agromyzidae	*Phytomyza enigmoides*	1	1	0.00	0.1236
Diptera	Agromyzidae	*Phytomyza evanescens*	2	2	0.45	-0.0999
Diptera	Anthomyiidae	*Adia cinerella*	1074	17	0.17	-0.1241
Diptera	Anthomyiidae	*Anthomyia confusanea*	6	3	0.09	-0.1638
Diptera	Anthomyiidae	*Anthomyia liturata*	47	13	0.14	0.1203
Diptera	Anthomyiidae	*Anthomyia pluvialis*	1	1	0.00	0.0434
Diptera	Anthomyiidae	*Botanophila biciliaris*	2	2	0.09	0.0763
Diptera	Anthomyiidae	*Botanophila brunneilinea*	7	4	0.22	-0.0898
Diptera	Anthomyiidae	*Botanophila discreta*	16	7	0.08	0.0654
Diptera	Anthomyiidae	*Botanophila fugax*	150	21	0.08	0.2444
Diptera	Anthomyiidae	*Botanophila striolata*	24	12	0.15	0.1267
Diptera	Anthomyiidae	*Botanophila varicolor*	3	2	0.14	-0.1274
Diptera	Anthomyiidae	*Calythea nigricans*	14	3	0.02	-0.0237
Diptera	Anthomyiidae	*Delia cf. nigrescens*	1	1	0.00	-0.0570
Diptera	Anthomyiidae	*Delia coarctata*	4	2	0.22	0.1352
Diptera	Anthomyiidae	*Delia echinata*	2	1	0.11	0.0763
Diptera	Anthomyiidae	*Delia florilega*	30	14	0.08	0.2006
Diptera	Anthomyiidae	*Delia nuda*	3	2	0.10	0.0708
Diptera	Anthomyiidae	*Delia platura*	63	13	0.16	0.1098
Diptera	Anthomyiidae	*Delia radicum*	19	7	0.08	0.1296
Diptera	Anthomyiidae	*Heterostylodes nominabilis*	46	6	0.41	-0.1963
Diptera	Anthomyiidae	*Heterostylodes obscurus*	4	2	0.23	-0.1438
Diptera	Anthomyiidae	*Heterostylodes pratensis*	2	2	0.67	0.0044
Diptera	Anthomyiidae	*Hydrophoria ruralis*	1	1	0.00	0.0068
Diptera	Anthomyiidae	*Hylemya partita*	1	1	0.00	-0.0541
Diptera	Anthomyiidae	*Hylemya urbica*	11	4	0.09	0.0463
Diptera	Anthomyiidae	*Hylemya vagans*	1	1	0.00	0.0830
Diptera	Anthomyiidae	*Hylemya variata*	19	6	0.17	-0.0242
Diptera	Anthomyiidae	*Lasiomma picipes*	2	2	0.00	0.0845
Diptera	Anthomyiidae	*Leucophora obtusa*	1	1	0.00	-0.1043
Diptera	Anthomyiidae	*Paregle audacula*	5	3	0.04	-0.0350
Diptera	Anthomyiidae	*Pegoplata aestiva*	456	37	0.34	0.0315
Diptera	Anthomyiidae	*Pegoplata infirma*	33	3	0.01	0.0769
Diptera	Anthomyiidae	*Phorbia fumigata*	1	1	0.00	0.0695
Diptera	Asilidae	*Didysmachus picipes*	1	1	0.00	0.0183
Diptera	Asilidae	*Leptogaster cylindrica*	5	5	0.29	0.0039
Diptera	Bibionidae	*Bibio hortulanus*	1	1	0.00	-0.0415
Diptera	Bibionidae	*Bibio johannis*	5	2	0.09	-0.0970
Diptera	Bibionidae	*Bibio marci*	2	2	0.00	0.1271
Diptera	Bibionidae	*Dilophus febrilis*	229	10	0.14	0.1103
Diptera	Bombyliidae	*Bombylella atra*	4	4	0.55	-0.1461
Diptera	Bombyliidae	*Bombylius canescens*	4	3	0.24	-0.1488
Diptera	Bombyliidae	*Bombylius venosus*	8	3	0.47	-0.0025
Diptera	Calliphoridae	*Bellardia pandia*	31	9	0.17	0.0651

Diptera	Calliphoridae	*Bellardia stricta*	1	1	0.00	0.0666
Diptera	Calliphoridae	*Bellardia viarum*	29	8	0.15	0.1786
Diptera	Calliphoridae	*Bellardia vulgaris*	25	9	0.19	0.1204
Diptera	Calliphoridae	*Calliphora vicina*	1	1	0.00	0.0357
Diptera	Calliphoridae	*Cynomya mortuorum*	51	9	0.13	0.0528
Diptera	Calliphoridae	*Eurychaeta palpalis*	11	1	0.03	0.0183
Diptera	Calliphoridae	*Lucilia bufonivora*	5	5	0.10	-0.0320
Diptera	Calliphoridae	*Lucilia caesar*	13	3	0.20	0.0514
Diptera	Calliphoridae	*Lucilia illustris*	1	1	0.00	0.0270
Diptera	Calliphoridae	*Lucilia pilosiventris*	30	3	0.08	0.0110
Diptera	Calliphoridae	*Lucilia richardsi*	73	10	0.11	-0.0821
Diptera	Calliphoridae	*Lucilia sericata*	7	5	0.11	0.0951
Diptera	Calliphoridae	*Lucilia silvarum*	316	18	0.12	0.1110
Diptera	Calliphoridae	*Melanomya nana*	6	1	0.14	0.1283
Diptera	Calliphoridae	*Melinda gentilis*	30	7	0.07	0.0718
Diptera	Calliphoridae	*Melinda viridicyanea*	43	11	0.08	0.1356
Diptera	Calliphoridae	*Morinia doronici*	1	1	0.00	0.0695
Diptera	Calliphoridae	*Onesia floralis*	37	5	0.14	0.1978
Diptera	Calliphoridae	*Pollenia amentaria*	245	17	0.13	0.1328
Diptera	Calliphoridae	*Pollenia angustigena*	7	3	0.00	0.1445
Diptera	Calliphoridae	*Pollenia hungarica*	5	3	0.00	0.0768
Diptera	Calliphoridae	*Pollenia labialis*	1	1	0.00	-0.0222
Diptera	Calliphoridae	*Pollenia moravica*	1	1	0.14	0.0183
Diptera	Calliphoridae	*Pollenia pediculata*	212	19	0.13	-0.0085
Diptera	Calliphoridae	*Pollenia rudis*	11	6	0.04	0.1548
Diptera	Calliphoridae	*Pollenia venturii*	3	2	0.15	-0.0006
Diptera	Calliphoridae	*Pollenia vera*	1	1	0.00	0.0434
Diptera	Calliphoridae	*Protocalliphora azurea*	5	3	0.04	-0.0098
Diptera	Calliphoridae	*Protophormia terraenovae*	1	1	0.00	0.0724
Diptera	Chloropidae	*Aphanotrigonum nigripes*	4	1	0.23	0.1187
Diptera	Chloropidae	*Cetema neglectum*	1	1	0.63	0.1294
Diptera	Chloropidae	*Chlorops elongata*	1	1	0.75	-0.0994
Diptera	Chloropidae	*Chlorops hypostigma*	31	6	0.21	0.0795
Diptera	Chloropidae	*Chlorops laetus*	5	1	0.63	0.0010
Diptera	Chloropidae	*Chlorops meigenii*	136	4	0.57	-0.1387
Diptera	Chloropidae	*Chlorops novakii*	1	1	0.07	-0.0106
Diptera	Chloropidae	*Chlorops pumilionis*	110	9	0.21	-0.0915
Diptera	Chloropidae	*Chlorops rossicus*	5	1	0.31	-0.0898
Diptera	Chloropidae	*Chlorops scalaris*	1	1	0.25	0.0956
Diptera	Chloropidae	*Chlorops serenus*	7	2	0.04	0.1504
Diptera	Chloropidae	*Chlorops speciosus*	1	1	0.03	-0.1168
Diptera	Chloropidae	*Lasiambia palposa*	1	1	0.24	0.0396
Diptera	Chloropidae	*Meromyza femorata*	58	13	0.27	0.1046
Diptera	Chloropidae	*Meromyza nigriventris*	6	3	0.12	-0.1045
Diptera	Chloropidae	*Meromyza saltatrix*	10	7	0.28	0.1396
Diptera	Chloropidae	*Microcercis albipalpis*	8	4	0.37	0.0820
Diptera	Chloropidae	*Oscinella frit*	172	22	0.19	-0.0239
Diptera	Chloropidae	*Oscinella maura*	10	7	0.22	-0.0546
Diptera	Chloropidae	*Oscinella nitidissima*	1	1	0.48	-0.0840
Diptera	Chloropidae	*Oscinimorpha koeleriae*	10	3	0.41	-0.1043
Diptera	Chloropidae	*Oscinimorpha minutissima*	28	9	0.24	-0.1489
Diptera	Chloropidae	*Oscinimorpha sordidissima*	3	3	0.36	-0.1644
Diptera	Chloropidae	*Siphonella oscinina*	3	2	0.25	-0.1412
Diptera	Chloropidae	*Syphonella oscinina*	10	3	0.54	-0.0305
Diptera	Chloropidae	*Trachysiphonella pygmaea*	123	16	0.36	-0.3260

Diptera	Chloropidae	*Trachysiphonella scutellata*	24	9	0.36	-0.1684
Diptera	Chloropidae	*Tricimba cincta*	1	1	0.03	-0.1168
Diptera	Conopidae	*Conops flavipes*	1	1	0.00	0.0724
Diptera	Conopidae	*Myopa testacea*	2	1	0.15	0.0224
Diptera	Conopidae	*Sicus ferrugineus*	6	3	0.13	-0.0368
Diptera	Conopidae	*Thecophora atra*	11	7	0.21	-0.0343
Diptera	Conopidae	*Thecophora distincta*	4	3	0.36	-0.0478
Diptera	Conopidae	*Thecophora pusilla*	2	2	0.08	-0.1602
Diptera	Dolichopodidae	*Poecilobothrus regalis*	1	1	0.00	0.0956
Diptera	Drosophilidae	*Scaptomyza pallida*	2	1	0.12	0.1168
Diptera	Empididae	*Empis albinervis*	3	2	0.05	-0.2055
Diptera	Empididae	*Empis dimidiata*	5	2	0.02	-0.0504
Diptera	Empididae	*Empis femorata*	1	1	0.00	0.0956
Diptera	Empididae	*Empis flavitarsis*	1	1	0.22	0.0010
Diptera	Empididae	*Empis grisea*	4	4	0.27	0.1599
Diptera	Empididae	*Empis livida*	335	28	0.34	-0.0985
Diptera	Empididae	*Empis nigripes*	112	9	0.13	0.2221
Diptera	Empididae	*Empis opaca*	31	3	0.02	-0.0270
Diptera	Empididae	*Empis s. str. aestiva*	17	12	0.34	-0.0576
Diptera	Empididae	*Empis s. str. caudatula*	54	9	0.34	0.0040
Diptera	Empididae	*Empis s. str. chioptera*	3	3	0.05	0.0664
Diptera	Empididae	*Empis s. str. nitidiventris*	2	1	0.08	0.1662
Diptera	Empididae	*Empis s. str. nuntia*	3	1	0.11	0.0135
Diptera	Empididae	*Empis s. str. planetica*	2	2	0.11	-0.0634
Diptera	Empididae	*Empis s. str. prodromus*	14	3	0.20	0.0267
Diptera	Empididae	*Empis s. str. pseudonuntia*	37	7	0.53	0.1882
Diptera	Empididae	*Empis sericans*	28	7	0.31	-0.1419
Diptera	Empididae	*Hilara clypeata*	6	3	0.00	0.0393
Diptera	Empididae	*Hilara longivittata*	53	3	0.15	0.1399
Diptera	Empididae	*Hilara pseudocornicula*	14	3	0.20	-0.0987
Diptera	Empididae	*Rhamphomyia longipes*	44	7	0.10	0.0019
Diptera	Empididae	*Rhamphomyia sulcata*	5	1	0.00	0.0843
Diptera	Empididae	*Rhamphomyia umbripennis*	22	4	0.27	-0.0565
Diptera	Fanniidae	*Fannia armata*	2	2	0.04	0.0492
Diptera	Fanniidae	*Fannia genualis*	1	1	0.00	0.1419
Diptera	Fanniidae	*Fannia latipalpis*	16	3	0.24	0.0191
Diptera	Fanniidae	*Fannia lepida*	2	2	0.01	-0.0213
Diptera	Fanniidae	*Fannia mollissima*	33	3	0.06	0.0492
Diptera	Fanniidae	*Fannia rondanii*	2	1	0.37	0.0492
Diptera	Fanniidae	*Fannia serena*	65	5	0.16	0.1885
Diptera	Fanniidae	*Fannia umbrosa*	5	1	0.01	0.1187
Diptera	Hybotidae	*Bicellaria spuria*	11	4	0.05	-0.0297
Diptera	Hybotidae	*Bicellaria sulcata*	2	1	0.00	-0.0475
Diptera	Hybotidae	*Platypalpus calceatus*	1	1	0.00	-0.0541
Diptera	Hybotidae	*Platypalpus infectus*	9	5	0.29	0.2076
Diptera	Lonchopteridae	*Lonchoptera bifurcata*	4	4	0.12	0.0554
Diptera	Lonchopteridae	*Lonchoptera lutea*	1	1	0.00	-0.0125
Diptera	Muscidae	*Azelia trigonica*	4	4	0.08	0.0041
Diptera	Muscidae	*Azelia triquetra*	2	1	0.00	0.0726
Diptera	Muscidae	*Coenosia albicornis*	4	3	0.33	0.0264
Diptera	Muscidae	*Coenosia infantula*	2	1	0.31	0.1172
Diptera	Muscidae	*Coenosia pedella*	51	8	0.15	0.0661
Diptera	Muscidae	*Coenosia pumila*	19	8	0.09	0.1129
Diptera	Muscidae	*Coenosia pygmaea*	1	1	0.77	0.0097
Diptera	Muscidae	*Coenosia testacea*	1	1	0.00	-0.1091

Diptera	Muscidae	*Coenosia tigrina*	12	6	0.18	0.0491
Diptera	Muscidae	*Coenosia verralli*	20	3	0.10	0.1487
Diptera	Muscidae	*Drymeia hamata*	4	2	0.20	0.0331
Diptera	Muscidae	*Eudasyphora cyanella*	1	1	0.00	0.0434
Diptera	Muscidae	*Eudasyphora cyanicolor*	8	5	0.21	-0.0988
Diptera	Muscidae	*Graphomya maculata*	3	2	0.00	0.0458
Diptera	Muscidae	*Haematobosca stimulans*	13	2	0.02	-0.0618
Diptera	Muscidae	*Helina impuncta*	4	2	0.00	-0.0224
Diptera	Muscidae	*Helina latitarsis*	16	4	0.11	0.1042
Diptera	Muscidae	*Helina reversio*	26	10	0.24	-0.0654
Diptera	Muscidae	*Helina trivittata*	15	5	0.14	0.0190
Diptera	Muscidae	*Hydrotaea albipuncta*	5	3	0.15	0.1275
Diptera	Muscidae	*Hydrotaea irritans*	1	1	0.00	-0.0666
Diptera	Muscidae	*Hydrotaea parva*	21	2	0.01	0.0190
Diptera	Muscidae	*Morellia aenescens*	216	13	0.14	0.1782
Diptera	Muscidae	*Morellia hortorum*	21	3	0.05	-0.0211
Diptera	Muscidae	*Morellia podagrica*	3	1	0.00	0.0194
Diptera	Muscidae	*Morellia simplex*	2	2	0.13	0.0225
Diptera	Muscidae	*Musca autumnalis*	313	23	0.19	0.1019
Diptera	Muscidae	*Musca osiris*	2	1	0.00	0.0434
Diptera	Muscidae	*Muscina levida*	4	1	0.65	0.1390
Diptera	Muscidae	*Muscina pascuorum*	2	1	0.17	0.0399
Diptera	Muscidae	*Myospila meditabunda*	2	1	0.03	0.0782
Diptera	Muscidae	*Neomyia cornicina*	168	16	0.10	0.0302
Diptera	Muscidae	*Neomyia viridescens*	75	9	0.07	0.0595
Diptera	Muscidae	*Phaonia angelicae*	13	4	0.11	0.0552
Diptera	Muscidae	*Phaonia meigeni*	2	1	0.00	0.0956
Diptera	Muscidae	*Phaonia serva*	8	4	0.12	0.1687
Diptera	Muscidae	*Polietes domitor*	5	1	0.00	0.0134
Diptera	Muscidae	*Polietes lardarius*	13	1	0.19	0.0053
Diptera	Muscidae	*Pyrellia rapax*	53	10	0.10	0.1040
Diptera	Muscidae	*Thricops longipes*	28	3	0.65	0.1440
Diptera	Muscidae	*Thricops nigrifrons*	10	4	0.17	0.1819
Diptera	Muscidae	*Thricops semicinereus*	1	1	0.00	0.1187
Diptera	Opomyzidae	*Geomyza tripunctata*	2	2	0.00	-0.0567
Diptera	Opomyzidae	*Opomyza florum*	82	5	0.05	0.0359
Diptera	Opomyzidae	*Opomyza germinationis*	1	1	0.00	0.0068
Diptera	Phoridae	*Conicera tibialis*	2	2	0.00	0.1134
Diptera	Phoridae	*Diplonevra funebris*	17	9	0.11	0.1239
Diptera	Phoridae	*Diplonevra nitidula*	16	3	0.19	0.0393
Diptera	Phoridae	*Megaselia brevicostalis*	7	5	0.28	0.0585
Diptera	Phoridae	*Megaselia vestita*	14	2	0.45	0.1390
Diptera	Phoridae	*Metopina galeata*	10	6	0.11	-0.1401
Diptera	Phoridae	*Metopina oligoneura*	319	19	0.46	0.0720
Diptera	Phoridae	*Metopina pileata*	14	3	0.50	-0.0113
Diptera	Phoridae	*Metopina ulrichi*	5	5	0.16	0.0382
Diptera	Rhagionidae	*Chrysopilus cristatus*	1	1	0.00	-0.0705
Diptera	Rhagionidae	*Rhagio vitripennis*	7	2	0.08	0.0695
Diptera	Rhinophoridae	*Rhinomorinia sarcophagina*	12	5	0.18	0.0320
Diptera	Rhinophoridae	*Rhinophora lepida*	3	2	0.21	0.0293
Diptera	Rhinophoridae	*Stevenia atramentaria*	15	4	0.10	0.1866
Diptera	Sarcophagidae	*Blaesoxipha erythrura*	1	1	0.36	0.1033
Diptera	Sarcophagidae	*Blaesoxipha plumicornis*	4	2	0.11	-0.0014
Diptera	Sarcophagidae	*Brachicoma devia*	1	1	0.00	0.1187
Diptera	Sarcophagidae	*Miltogramma germari*	1	1	0.00	0.0270

Diptera	Sarcophagidae	*Nyctia halterata*	3	2	0.11	-0.1704
Diptera	Sarcophagidae	*Paramacronychia flavipalpis*	6	4	0.12	0.0692
Diptera	Sarcophagidae	*Ravinia pernix*	8	2	0.08	0.0848
Diptera	Sarcophagidae	*Sarcophaga aratrix*	1	1	0.00	0.1101
Diptera	Sarcophagidae	*Sarcophaga caerulescens*	1	1	0.00	-0.0386
Diptera	Sarcophagidae	*Sarcophaga carnaria*	453	34	0.18	0.1501
Diptera	Sarcophagidae	*Sarcophaga crassimargo*	27	5	0.08	0.0674
Diptera	Sarcophagidae	*Sarcophaga depressifrons*	2	2	0.16	0.0222
Diptera	Sarcophagidae	*Sarcophaga dissimilis*	2	2	0.00	0.0882
Diptera	Sarcophagidae	*Sarcophaga haemorrhoa*	3	2	0.00	0.1233
Diptera	Sarcophagidae	*Sarcophaga incisilobata*	30	7	0.16	0.0401
Diptera	Sarcophagidae	*Sarcophaga melanura*	3	3	0.00	0.0113
Diptera	Sarcophagidae	*Sarcophaga nigriventris*	11	3	0.19	-0.0252
Diptera	Sarcophagidae	*Sarcophaga noverca*	6	2	0.05	0.0561
Diptera	Sarcophagidae	*Sarcophaga pumila*	20	8	0.11	0.0644
Diptera	Sarcophagidae	*Sarcophaga sinuata*	5	1	0.36	0.1836
Diptera	Sarcophagidae	*Sarcophaga subvicina*	53	8	0.11	0.1205
Diptera	Sarcophagidae	*Sarcophaga vagans*	1	1	0.01	0.1342
Diptera	Sarcophagidae	*Sarcophaga variegata*	309	24	0.15	0.2768
Diptera	Sarcophagidae	*Sarcophaga vicina*	3	3	0.28	0.0591
Diptera	Scathophagidae	*Scathophaga inquinata*	1	1	0.00	-0.0048
Diptera	Scathophagidae	*Scathophaga stercoraria*	27	5	0.03	0.0729
Diptera	Scatopsidae	*Coboldia fuscipes*	4	3	0.00	-0.0692
Diptera	Scatopsidae	*Swammerdamella brevicornis*	13	4	0.24	0.1060
Diptera	Sciaridae	*Bradysia pallipes*	2	1	0.10	-0.0415
Diptera	Sciaridae	*Bradysia vagans*	1	1	0.00	-0.1043
Diptera	Sciaridae	*Schwenckfeldina carbonaria*	8	2	0.17	0.0972
Diptera	Sciaridae	*Sciara flavimana*	2	2	0.37	-0.0039
Diptera	Sepsidae	*Saltella sphondylii*	18	7	0.17	-0.0999
Diptera	Sepsidae	*Sepsis cynipsea*	34	9	0.18	0.0531
Diptera	Sepsidae	*Sepsis fulgens*	28	5	0.05	0.0075
Diptera	Sepsidae	*Sepsis orthocnemis*	3	2	0.00	-0.0639
Diptera	Sepsidae	*Sepsis violacea*	7	3	0.01	0.0637
Diptera	Sepsidae	*Themira minor*	5	1	0.00	0.1236
Diptera	Stratiomyidae	*Chloromyia formosa*	90	10	0.23	0.1132
Diptera	Stratiomyidae	*Microchrysa flavicornis*	1	1	0.03	-0.0898
Diptera	Stratiomyidae	*Nemotelus nigrinus*	6	3	0.01	0.0877
Diptera	Stratiomyidae	*Nemotelus pantherinus*	114	7	0.14	-0.0147
Diptera	Stratiomyidae	*Oplodontha viridula*	10	7	0.07	0.0539
Diptera	Stratiomyidae	*Pachygaster atra*	3	1	0.00	0.0434
Diptera	Stratiomyidae	*Stratiomys ornata*	1	1	0.00	0.0270
Diptera	Syrphidae	*Anasimyia interpuncta*	1	1	0.00	0.0097
Diptera	Syrphidae	*Anasimyia lineata*	5	4	0.09	0.1320
Diptera	Syrphidae	*Chalcosyrphus nemorum*	3	2	0.36	-0.0051
Diptera	Syrphidae	*Cheilosia albitarsis*	15	2	0.23	-0.0135
Diptera	Syrphidae	*Cheilosia barbata*	2	2	0.26	-0.0428
Diptera	Syrphidae	*Cheilosia carbonaria*	1	1	0.00	0.0270
Diptera	Syrphidae	*Cheilosia chloris*	3	1	0.00	-0.0463
Diptera	Syrphidae	*Cheilosia illustrata*	3	2	0.03	0.0896
Diptera	Syrphidae	*Cheilosia impressa*	4	1	0.09	0.0415
Diptera	Syrphidae	*Cheilosia latifrons*	2	2	0.08	0.1052
Diptera	Syrphidae	*Cheilosia pagana*	57	14	0.30	0.1615
Diptera	Syrphidae	*Cheilosia scutellata*	1	1	0.00	0.0222
Diptera	Syrphidae	*Cheilosia soror*	1	1	0.00	-0.0386
Diptera	Syrphidae	*Cheilosia vernalis-agg.*	7	4	0.15	-0.1087

Diptera	Syrphidae	*Cheilosia vulpina*	9	3	0.06	0.0389
Diptera	Syrphidae	*Chrysogaster coemiteriorum*	1	1	0.00	-0.0956
Diptera	Syrphidae	*Chrysogaster solstitialis*	7	5	0.34	0.1203
Diptera	Syrphidae	*Chrysogaster virescens*	2	2	0.57	0.0528
Diptera	Syrphidae	*Chrysotoxum bicinctum*	47	19	0.21	-0.0126
Diptera	Syrphidae	*Chrysotoxum cautum*	2	2	0.06	0.0910
Diptera	Syrphidae	*Chrysotoxum elegans*	1	1	0.00	0.0068
Diptera	Syrphidae	*Chrysotoxum festivum*	27	9	0.21	0.0350
Diptera	Syrphidae	*Chrysotoxum verralli*	1	1	0.37	0.1129
Diptera	Syrphidae	*Dasysyrphus hilaris*	3	3	0.55	-0.0151
Diptera	Syrphidae	*Dasysyrphus pinastri*	1	1	0.00	0.1072
Diptera	Syrphidae	*Epistrophe grossulariae*	3	1	0.00	0.1154
Diptera	Syrphidae	*Epistrophe nitidicollis*	5	4	0.16	0.0489
Diptera	Syrphidae	*Episyrphus balteatus*	929	61	0.29	0.0766
Diptera	Syrphidae	*Eriozona syrphoides*	1	1	0.00	0.0357
Diptera	Syrphidae	*Eristalinus aeneus*	4	3	0.11	-0.0580
Diptera	Syrphidae	*Eristalinus sepulchralis*	79	15	0.15	0.0004
Diptera	Syrphidae	*Eristalis abusiva*	44	12	0.10	0.0086
Diptera	Syrphidae	*Eristalis arbustorum*	106	18	0.09	0.0948
Diptera	Syrphidae	*Eristalis interrupta*	59	16	0.14	0.1299
Diptera	Syrphidae	*Eristalis intricaria*	10	5	0.17	-0.0201
Diptera	Syrphidae	*Eristalis lineata*	9	5	0.17	0.0249
Diptera	Syrphidae	*Eristalis pertinax*	12	4	0.04	0.0611
Diptera	Syrphidae	*Eristalis pseudorupium*	8	4	0.07	0.0592
Diptera	Syrphidae	*Eristalis tenax*	298	30	0.22	0.0661
Diptera	Syrphidae	*Eumerus strigatus*	1	1	0.75	-0.1284
Diptera	Syrphidae	*Eumerus tricolor*	2	2	0.15	-0.0266
Diptera	Syrphidae	*Eupeodes bucculatus*	4	2	0.18	0.1223
Diptera	Syrphidae	*Eupeodes corollae*	88	29	0.18	0.0758
Diptera	Syrphidae	*Eupeodes lapponicus*	5	5	0.07	0.1296
Diptera	Syrphidae	*Eupeodes latifasciatus*	41	19	0.17	0.1084
Diptera	Syrphidae	*Eupeodes luniger*	15	10	0.16	0.1207
Diptera	Syrphidae	*Ferdinandea cuprea*	1	1	0.37	0.1129
Diptera	Syrphidae	*Helophilus hybridus*	25	8	0.06	0.0295
Diptera	Syrphidae	*Helophilus pendulus*	35	12	0.15	0.1014
Diptera	Syrphidae	*Helophilus trivittatus*	47	15	0.11	-0.1111
Diptera	Syrphidae	*Heringia latitarsis*	1	1	0.00	0.1149
Diptera	Syrphidae	*Lejogaster metallina*	5	3	0.47	0.0081
Diptera	Syrphidae	*Lejogaster tarsata*	1	1	0.58	-0.0705
Diptera	Syrphidae	*Leucozona glaucia*	1	1	0.00	-0.0164
Diptera	Syrphidae	*Leucozona laternaria*	1	1	0.00	0.0434
Diptera	Syrphidae	*Melangyna umbellatarum*	6	4	0.11	0.1325
Diptera	Syrphidae	*Melanogaster aerosa / parumplicata*	1	1	0.00	-0.0956
Diptera	Syrphidae	*Melanogaster nuda*	60	5	0.22	-0.0851
Diptera	Syrphidae	*Melanostoma mellinum-agg.*	204	38	0.31	0.2337
Diptera	Syrphidae	*Melanostoma scalare*	5	4	0.47	0.0386
Diptera	Syrphidae	*Meliscaeva cinctella*	4	2	0.00	-0.0047
Diptera	Syrphidae	*Merodon armipes*	23	3	0.24	0.0198
Diptera	Syrphidae	*Merodon rufus*	1	1	0.01	-0.1091
Diptera	Syrphidae	*Myathropa florea*	37	9	0.09	0.1995
Diptera	Syrphidae	*Neoascia obliqua*	3	3	0.21	-0.0512
Diptera	Syrphidae	*Neoascia tenur*	3	2	0.16	0.0293
Diptera	Syrphidae	*Neoascia unifasciata*	1	1	0.00	-0.0512
Diptera	Syrphidae	*Paragus haemorrhous*	1	1	0.00	-0.1361

Diptera	Syrphidae	*Parasyrphus annulatus*	3	2	0.09	-0.0157
Diptera	Syrphidae	*Parasyrphus lineolus*	9	3	0.20	-0.0543
Diptera	Syrphidae	*Parasyrphus vittiger*	2	2	0.75	-0.0622
Diptera	Syrphidae	*Pipiza bimaculata*	3	2	0.00	-0.0110
Diptera	Syrphidae	*Pipiza noctiluca*	9	8	0.21	-0.0058
Diptera	Syrphidae	*Pipiza quadrimaculata*	14	3	0.32	0.1790
Diptera	Syrphidae	*Pipizella viduata*	39	14	0.23	-0.0752
Diptera	Syrphidae	*Platycheirus albimanus*	240	40	0.21	0.2330
Diptera	Syrphidae	*Platycheirus clypeatus*	27	14	0.46	0.2070
Diptera	Syrphidae	*Platycheirus europaeus*	8	1	0.03	0.1096
Diptera	Syrphidae	*Platycheirus fulviventris*	1	1	0.00	-0.0261
Diptera	Syrphidae	*Platycheirus granditarsis*	3	3	0.08	0.0538
Diptera	Syrphidae	*Platycheirus manicatus*	3	3	0.20	0.0347
Diptera	Syrphidae	*Platycheirus peltatus*	27	13	0.19	-0.0239
Diptera	Syrphidae	*Platycheirus scutatus*	4	4	0.17	0.0623
Diptera	Syrphidae	*Rhingia campestris*	19	9	0.44	-0.0377
Diptera	Syrphidae	*Scaeva dignota*	1	1	0.00	0.0270
Diptera	Syrphidae	*Scaeva pyrastri*	46	15	0.21	-0.0599
Diptera	Syrphidae	*Scaeva selenitica*	18	9	0.08	-0.0653
Diptera	Syrphidae	*Sphaerophoria bankowskae*	1	1	0.25	-0.1014
Diptera	Syrphidae	*Sphaerophoria batava*	1	1	0.37	0.0743
Diptera	Syrphidae	*Sphaerophoria interrupta-Gruppe*	553	65	0.28	0.1075
Diptera	Syrphidae	*Sphaerophoria scripta*	1137	80	0.24	0.0961
Diptera	Syrphidae	*Sphaerophoria taeniata*	267	44	0.31	0.0923
Diptera	Syrphidae	*Syritta pipiens*	227	17	0.20	0.1402
Diptera	Syrphidae	*Syrphus ribesii*	216	35	0.18	0.1666
Diptera	Syrphidae	*Syrphus torvus*	89	23	0.15	0.1544
Diptera	Syrphidae	*Syrphus vitripennis*	112	16	0.14	0.1867
Diptera	Syrphidae	*Temnostoma bombylans*	1	1	0.62	-0.0241
Diptera	Syrphidae	*Tropidia scita*	20	3	0.03	-0.0908
Diptera	Syrphidae	*Volucella bombylans*	16	9	0.09	-0.1624
Diptera	Syrphidae	*Volucella pellucens*	1	1	0.00	0.0270
Diptera	Syrphidae	*Xanthogramma citrofasciatum*	1	1	0.00	-0.0666
Diptera	Syrphidae	*Xanthogramma pedissequum*	3	3	0.15	-0.0077
Diptera	Syrphidae	*Xylota jakutorum*	1	1	0.50	-0.1390
Diptera	Tabanidae	*Haematopota pluvialis*	3	2	0.10	-0.0539
Diptera	Tachinidae	*Allophorocera ferruginea*	10	1	0.04	0.0896
Diptera	Tachinidae	*Bithia spreta*	1	1	0.00	-0.0386
Diptera	Tachinidae	*Blondelia nigripes*	3	1	0.00	0.0134
Diptera	Tachinidae	*Cistogaster globosa*	4	1	0.09	-0.1011
Diptera	Tachinidae	*Cylindromyia auriceps*	1	1	0.33	-0.0290
Diptera	Tachinidae	*Cylindromyia brassicaria*	7	4	0.19	-0.0646
Diptera	Tachinidae	*Dinera ferina*	4	3	0.14	0.0433
Diptera	Tachinidae	*Dinera grisescens*	1	1	0.54	0.0830
Diptera	Tachinidae	*Drino vicina*	1	1	0.00	0.0068
Diptera	Tachinidae	*Dufouria chalybeata*	2	2	0.50	-0.0216
Diptera	Tachinidae	*Dufouria nigrita*	1	1	0.20	-0.0203
Diptera	Tachinidae	*Ectophasia oblonga*	6	3	0.08	-0.0337
Diptera	Tachinidae	*Eloceria delecta*	1	1	0.13	-0.1149
Diptera	Tachinidae	*Eriothrix rufomaculatus*	13	6	0.24	0.1717
Diptera	Tachinidae	*Estheria cristata*	5	4	0.25	-0.0724
Diptera	Tachinidae	*Eurithia vivida*	1	1	0.17	-0.1265
Diptera	Tachinidae	*Exorista rustica*	9	4	0.29	-0.0466
Diptera	Tachinidae	*Exorista tubulosa*	1	1	0.00	0.0357
Diptera	Tachinidae	*Fausta nemorum*	1	1	0.00	0.1168

Diptera	Tachinidae	*Gonia capitata*	13	5	0.22	-0.1342
Diptera	Tachinidae	*Gymnosoma clavatum*	3	1	0.11	-0.0580
Diptera	Tachinidae	*Gymnosoma nitens*	4	3	0.11	-0.2017
Diptera	Tachinidae	*Gymnosoma nudifrons*	1	1	1.00	-0.0048
Diptera	Tachinidae	*Gymnosoma rotundatum*	3	1	0.09	-0.0045
Diptera	Tachinidae	*Leucostoma simplex*	11	7	0.10	0.0402
Diptera	Tachinidae	*Linnaemya picta*	1	1	0.00	-0.0164
Diptera	Tachinidae	*Macquartia dispar*	1	1	0.00	-0.0541
Diptera	Tachinidae	*Macquartia praefica*	9	2	0.11	-0.0716
Diptera	Tachinidae	*Meigenia mutabilis-Gruppe*	2	2	0.08	0.0442
Diptera	Tachinidae	*Ocytata pallipes*	1	1	0.17	0.0763
Diptera	Tachinidae	*Opesia cana*	1	1	0.00	-0.0125
Diptera	Tachinidae	*Phania curvicauda*	1	1	0.00	-0.0203
Diptera	Tachinidae	*Phania funesta*	1	1	0.00	-0.0048
Diptera	Tachinidae	*Phasia barbifrons*	1	1	0.05	-0.0782
Diptera	Tachinidae	*Phasia hemiptera*	17	5	0.11	0.1092
Diptera	Tachinidae	*Phasia obesa*	45	6	0.13	-0.1242
Diptera	Tachinidae	*Phasia pusilla*	2	2	0.00	0.0262
Diptera	Tachinidae	*Phryxe nemea*	1	1	0.10	0.0560
Diptera	Tachinidae	*Phryxe vulgaris*	9	5	0.21	0.0420
Diptera	Tachinidae	*Phytomyptera minutissima*	1	1	0.00	0.0357
Diptera	Tachinidae	*Prosena siberita*	3	2	0.26	0.0805
Diptera	Tachinidae	*Rondania dimidiata*	1	1	0.03	-0.1168
Diptera	Tachinidae	*Siphona geniculata*	65	16	0.31	0.1237
Diptera	Tachinidae	*Solieria fenestrata*	1	1	0.00	0.0724
Diptera	Tachinidae	*Solieria pacifica*	15	6	0.23	0.1015
Diptera	Tachinidae	*Tachina fera*	30	3	0.05	0.0278
Diptera	Tachinidae	*Voria ruralis*	5	4	0.22	0.0415
Diptera	Tachinidae	*Zeuxia cinerea*	3	3	0.00	-0.0431
Diptera	Tachinidae	*Zophomyia temula*	2	1	0.00	0.0138
Diptera	Tephritidae	*Chaetorellia jaceae*	2	2	0.00	-0.0166
Diptera	Tephritidae	*Dioxyna bidentis*	1	1	0.00	0.0666
Diptera	Tephritidae	*Ensina sonchi*	3	2	0.59	0.1538
Diptera	Tephritidae	*Orellia falcata*	6	4	0.51	-0.1101
Diptera	Tephritidae	*Oxyna flavipennis*	49	8	0.23	0.0831
Diptera	Tephritidae	*Terellia tussilaginis*	1	1	0.00	0.1342
Diptera	Tephritidae	*Urophora cardui*	1	1	0.03	-0.1390
Diptera	Tephritidae	*Urophora quadrifasciata*	1	1	0.03	-0.1168
Diptera	Tipulidae	*Lunatipula vernalis*	104	2	0.14	0.1380
Diptera	Tipulidae	*Nephrotoma appendiculata*	34	1	0.24	0.0395
Diptera	Tipulidae	*Nephrotoma flavescens*	4	2	0.05	0.2029
Diptera	Ulidiidae	*Physiphora alceae*	5	2	0.01	-0.0386
Hymenoptera	Apidae	*Andrena bicolor*	20	4	0.46	0.0521
Hymenoptera	Apidae	*Andrena carantonica*	2	2	0.17	0.0140
Hymenoptera	Apidae	*Andrena chrysosceles*	19	6	0.10	-0.0163
Hymenoptera	Apidae	*Andrena cineraria*	4	4	0.00	0.0194
Hymenoptera	Apidae	*Andrena denticulata*	1	1	0.82	-0.0338
Hymenoptera	Apidae	*Andrena dorsata*	7	1	0.02	0.0270
Hymenoptera	Apidae	*Andrena falsifica*	1	1	0.70	0.0183
Hymenoptera	Apidae	*Andrena flavipes*	47	8	0.12	0.0704
Hymenoptera	Apidae	*Andrena fucata*	3	2	0.32	0.0111
Hymenoptera	Apidae	*Andrena fulvago*	3	3	0.33	-0.0169
Hymenoptera	Apidae	*Andrena gelriae*	2	2	0.01	-0.0922
Hymenoptera	Apidae	*Andrena gravida*	7	4	0.10	0.0573
Hymenoptera	Apidae	*Andrena haemorrhoa*	66	5	0.11	0.1370

Hymenoptera	Apidae	*Andrena intermedia*	1	1	0.00	-0.1091
Hymenoptera	Apidae	*Andrena labialis*	13	4	0.09	0.1017
Hymenoptera	Apidae	*Andrena minutuloides*	5	4	0.06	-0.0388
Hymenoptera	Apidae	*Andrena nigroaenea*	5	4	0.13	0.0086
Hymenoptera	Apidae	*Andrena nitida*	24	8	0.27	0.0337
Hymenoptera	Apidae	*Andrena ovatula*	4	2	0.25	0.0199
Hymenoptera	Apidae	*Andrena pilipes s. l.*	1	1	0.00	-0.0125
Hymenoptera	Apidae	*Andrena praecox*	1	1	0.00	-0.0125
Hymenoptera	Apidae	*Andrena proxima*	2	1	0.00	0.1120
Hymenoptera	Apidae	*Andrena semilaevis*	16	7	0.15	0.1270
Hymenoptera	Apidae	*Andrena subopaca*	27	10	0.42	0.1022
Hymenoptera	Apidae	*Andrena tibialis*	1	1	0.00	-0.0125
Hymenoptera	Apidae	*Andrena vaga*	2	1	0.00	0.1294
Hymenoptera	Apidae	*Andrena ventralis*	1	1	0.00	-0.0956
Hymenoptera	Apidae	*Andrena wilkella*	17	2	0.11	0.0661
Hymenoptera	Apidae	*Anthophora plumipes*	6	3	0.43	0.0615
Hymenoptera	Apidae	*Apis mellifera*	1655	45	0.47	0.0824
Hymenoptera	Apidae	*Bombus barbutellus*	1	1	0.00	0.0396
Hymenoptera	Apidae	*Bombus bohemicus*	26	6	0.27	0.0466
Hymenoptera	Apidae	*Bombus campestris*	4	2	0.44	0.0156
Hymenoptera	Apidae	*Bombus cryptarum*	12	3	0.37	0.1174
Hymenoptera	Apidae	*Bombus hortorum*	126	17	0.43	0.0620
Hymenoptera	Apidae	*Bombus humilis*	215	25	0.37	0.0284
Hymenoptera	Apidae	*Bombus hypnorum*	4	3	0.40	-0.0422
Hymenoptera	Apidae	*Bombus jonellus*	1	1	0.00	0.1149
Hymenoptera	Apidae	*Bombus lapidarius*	1039	50	0.39	-0.0302
Hymenoptera	Apidae	*Bombus lucorum*	216	20	0.29	0.1137
Hymenoptera	Apidae	*Bombus muscorum*	3	3	0.09	-0.0261
Hymenoptera	Apidae	*Bombus pascuorum*	838	50	0.47	0.1161
Hymenoptera	Apidae	*Bombus pratorum*	49	9	0.24	0.1975
Hymenoptera	Apidae	*Bombus ruderarius*	45	13	0.35	0.0756
Hymenoptera	Apidae	*Bombus rupestris*	32	10	0.45	-0.0797
Hymenoptera	Apidae	*Bombus semenoviellus*	2	2	0.07	0.0409
Hymenoptera	Apidae	*Bombus soroeensis*	240	28	0.28	0.0704
Hymenoptera	Apidae	*Bombus subterraneus*	22	4	0.26	0.0680
Hymenoptera	Apidae	*Bombus sylvarum*	449	50	0.42	0.0778
Hymenoptera	Apidae	*Bombus sylvestris*	1	1	0.70	0.0492
Hymenoptera	Apidae	*Bombus terrestris*	285	36	0.28	-0.0565
Hymenoptera	Apidae	*Bombus vestalis*	1	1	0.00	0.0994
Hymenoptera	Apidae	*Bombus veteranus*	1	1	0.59	0.0097
Hymenoptera	Apidae	*Bombus wurflenii*	50	7	0.49	0.0596
Hymenoptera	Apidae	*Ceratina cyanea*	1	1	0.18	-0.1390
Hymenoptera	Apidae	*Chalicodoma ericetorum*	1	1	0.63	-0.1091
Hymenoptera	Apidae	*Chelostoma florisomne*	3	2	0.19	0.0312
Hymenoptera	Apidae	*Chelostoma rapunculi*	1	1	0.85	0.1033
Hymenoptera	Apidae	*Colletes cunicularius*	6	1	0.05	-0.0295
Hymenoptera	Apidae	*Colletes marginatus*	2	2	0.26	0.1149
Hymenoptera	Apidae	*Dasypoda altercator*	31	4	0.24	0.0339
Hymenoptera	Apidae	*Eucera longicornis*	1	1	0.82	0.1101
Hymenoptera	Apidae	*Eucera nigrescens*	1	1	0.00	-0.1419
Hymenoptera	Apidae	*Halictus eurygnathus*	1	1	0.00	0.0183
Hymenoptera	Apidae	*Halictus maculatus*	7	2	0.25	0.0631
Hymenoptera	Apidae	*Halictus quadricinctus*	5	4	0.06	0.0306
Hymenoptera	Apidae	*Halictus rubicundus*	6	6	0.17	-0.0133
Hymenoptera	Apidae	*Halictus sexcinctus*	13	3	0.19	-0.0004

Hymenoptera	Apidae	*Halictus simplex s.l.*	13	4	0.36	-0.1007
Hymenoptera	Apidae	*Halictus tumulorum*	91	30	0.33	-0.2141
Hymenoptera	Apidae	*Hoplitis leucomelana*	1	1	0.34	-0.1390
Hymenoptera	Apidae	*Hoplosmia spinulosa*	2	1	0.07	-0.1245
Hymenoptera	Apidae	*Hylaeus annularis*	3	3	0.24	-0.1064
Hymenoptera	Apidae	*Hylaeus communis*	2	2	0.02	-0.0131
Hymenoptera	Apidae	*Hylaeus confusus*	5	3	0.50	0.0246
Hymenoptera	Apidae	*Hylaeus cornutus*	1	1	0.00	0.0724
Hymenoptera	Apidae	*Hylaeus difformis*	1	1	0.01	0.0328
Hymenoptera	Apidae	*Hylaeus gredleri*	8	4	0.29	0.1741
Hymenoptera	Apidae	*Hylaeus hyalinatus*	1	1	0.09	0.0010
Hymenoptera	Apidae	*Hylaeus signatus*	1	1	0.28	-0.0048
Hymenoptera	Apidae	*Lasioglossum albipes*	22	14	0.32	-0.2225
Hymenoptera	Apidae	*Lasioglossum calceatum*	204	38	0.26	-0.1622
Hymenoptera	Apidae	*Lasioglossum fulvicorne*	78	22	0.29	-0.2035
Hymenoptera	Apidae	*Lasioglossum laevigatum*	3	3	0.24	0.1468
Hymenoptera	Apidae	*Lasioglossum laticeps*	28	11	0.17	-0.0939
Hymenoptera	Apidae	*Lasioglossum lativentre*	23	7	0.30	0.1404
Hymenoptera	Apidae	*Lasioglossum leucopus*	6	5	0.14	-0.1867
Hymenoptera	Apidae	*Lasioglossum leucozonium*	7	3	0.12	-0.1321
Hymenoptera	Apidae	*Lasioglossum lineare*	22	4	0.41	0.0560
Hymenoptera	Apidae	*Lasioglossum malachurum*	12	5	0.15	-0.0629
Hymenoptera	Apidae	*Lasioglossum minutulum*	23	10	0.41	-0.0813
Hymenoptera	Apidae	*Lasioglossum morio*	7	5	0.44	-0.1437
Hymenoptera	Apidae	*Lasioglossum pauxillum*	227	36	0.25	-0.1553
Hymenoptera	Apidae	*Lasioglossum quadrinotatum*	4	3	0.25	0.1501
Hymenoptera	Apidae	*Lasioglossum villosulum*	15	7	0.23	-0.1295
Hymenoptera	Apidae	*Megachile alpicola*	2	2	0.13	-0.0717
Hymenoptera	Apidae	*Megachile centuncularis*	1	1	0.46	0.0270
Hymenoptera	Apidae	*Megachile circumcincta*	2	1	0.16	-0.1419
Hymenoptera	Apidae	*Megachile versicolor*	1	1	0.18	-0.1390
Hymenoptera	Apidae	*Melitta leporina*	14	4	0.40	-0.0224
Hymenoptera	Apidae	*Nomada fabriciana*	3	1	0.05	0.0357
Hymenoptera	Apidae	*Nomada fulvicornis*	3	3	0.20	-0.0119
Hymenoptera	Apidae	*Nomada integra*	2	2	0.67	0.0290
Hymenoptera	Apidae	*Nomada ruficornis*	1	1	0.01	0.0830
Hymenoptera	Apidae	*Nomada striata*	1	1	1.00	-0.0106
Hymenoptera	Apidae	*Osmia leaiana*	1	1	0.31	0.0010
Hymenoptera	Apidae	*Osmia xanthomelana*	2	1	0.06	-0.1091
Hymenoptera	Apidae	*Panurgus calcaratus*	23	3	0.35	0.1090
Hymenoptera	Apidae	*Sphecodes albilabris*	2	2	0.02	0.0588
Hymenoptera	Apidae	*Sphecodes crassus*	1	1	0.00	-0.0386
Hymenoptera	Apidae	*Sphecodes ephippius*	20	8	0.11	-0.0612
Hymenoptera	Apidae	*Sphecodes ferruginatus*	1	1	0.22	0.0010
Hymenoptera	Apidae	*Sphecodes hyalinatus*	3	3	0.21	-0.0676
Hymenoptera	Apidae	*Sphecodes monilicornis*	1	1	0.00	0.0029
Hymenoptera	Apidae	*Trachusa byssinum*	30	9	0.56	-0.1937
Hymenoptera	Argidae	*Arge dimidiata*	3	2	0.11	-0.1149
Hymenoptera	Argidae	*Arge melanochroa*	5	2	0.41	-0.0528
Hymenoptera	Argidae	*Arge rosae*	1	1	0.08	0.0068
Hymenoptera	Cephidae	*Calameuta filiformis*	3	1	0.00	-0.0048
Hymenoptera	Cephidae	*Cephus pygmaeus*	7	3	0.39	0.1349
Hymenoptera	Crabronidae	*Cerceris arenaria*	1	1	0.00	0.0270
Hymenoptera	Crabronidae	*Cerceris rybyensis*	6	3	0.31	0.0241
Hymenoptera	Crabronidae	*Crossocerus assimilis*	1	1	0.07	0.1390

Hymenoptera	Crabronidae	*Ectemnius borealis*	1	1	0.42	0.0299
Hymenoptera	Crabronidae	*Ectemnius continuus*	1	1	0.00	0.1342
Hymenoptera	Crabronidae	*Ectemnius lapidarius*	2	2	0.04	0.0365
Hymenoptera	Crabronidae	*Lindenius albilabris*	7	3	0.16	0.0679
Hymenoptera	Crabronidae	*Pemphredon inornata*	1	1	0.50	-0.1168
Hymenoptera	Crabronidae	*Philanthus triangulum*	1	1	0.00	0.0270
Hymenoptera	Diplazontinae	*Sussaba erigator*	1	1	0.07	-0.0627
Hymenoptera	Diplazontinae	*Syrphophilus bizonarius*	1	1	0.23	0.1294
Hymenoptera	Eupelmidae	*Eupelmus cf. vesicularis*	1	1	0.08	-0.0840
Hymenoptera	Formicidae	*Formica cunicularia*	210	18	0.31	-0.3192
Hymenoptera	Formicidae	*Formica rufibarbis*	125	14	0.29	-0.2895
Hymenoptera	Formicidae	*Lasius emarginatus*	9	3	0.55	-0.1624
Hymenoptera	Formicidae	*Lasius flavus*	1	1	0.00	0.0666
Hymenoptera	Formicidae	*Lasius niger*	785	35	0.31	-0.3235
Hymenoptera	Formicidae	*Lasius psammophilus*	3	3	0.32	-0.0869
Hymenoptera	Formicidae	*Myrmica gallienii*	2	1	0.13	-0.0840
Hymenoptera	Formicidae	*Myrmica rubra*	133	8	0.28	-0.0563
Hymenoptera	Formicidae	*Myrmica ruginodis*	1	1	0.00	0.1168
Hymenoptera	Formicidae	*Myrmica rugulosa*	34	1	0.35	-0.0840
Hymenoptera	Formicidae	*Myrmica scabrinodis*	2	1	0.20	-0.1168
Hymenoptera	Formicidae	*Tapinoma ambiguum*	4	4	0.20	-0.1239
Hymenoptera	Formicidae	*Tapinoma erraticum*	6	3	0.26	-0.0411
Hymenoptera	Ichneumonidae	*Amblyteles armatorius*	4	3	0.44	0.0809
Hymenoptera	Ichneumonidae	*Glyphicnemis sp.*	5	1	0.45	0.1390
Hymenoptera	Ichneumonidae	*Scambus cf. buolianae*	1	1	0.00	-0.0261
Hymenoptera	Sphecidae	*Cerceris ruficornis*	1	1	0.00	0.0270
Hymenoptera	Sphecidae	*Ectemnius ruficornis*	1	1	0.00	0.1187
Hymenoptera	Tenthredinidae	*Athalia ancilla*	3	2	0.61	0.1300
Hymenoptera	Tenthredinidae	*Athalia circularis*	1	1	0.47	-0.0898
Hymenoptera	Tenthredinidae	*Athalia rosae*	106	10	0.16	-0.0011
Hymenoptera	Tenthredinidae	*Cladius pectinicornis*	1	1	0.18	-0.1168
Hymenoptera	Tenthredinidae	*Dolerus asper*	3	1	0.09	0.0415
Hymenoptera	Tenthredinidae	*Dolerus carbonarius*	1	1	0.00	0.0415
Hymenoptera	Tenthredinidae	*Macrophya annulata*	6	5	0.54	0.1298
Hymenoptera	Tenthredinidae	*Selandria serva*	8	4	0.09	0.1376
Hymenoptera	Tenthredinidae	*Tenthredo arcuata*	1	1	0.00	0.0492
Hymenoptera	Tenthredinidae	*Tenthredo notha*	102	13	0.24	0.0534
Hymenoptera	Tiphiidae	*Tiphia femorata*	2	2	0.00	-0.0203
Hymenoptera	Vespidae	*Gymnomerus laevipes*	1	1	0.41	-0.0048
Hymenoptera	Vespidae	*Polistes dominulus*	3	1	0.05	0.0357
Lepidoptera	Crambidae	*Pyrausta purpuralis*	30	13	0.27	-0.1702
Lepidoptera	Geometridae	*Chiasmia clathrata*	2	2	0.09	0.0966
Lepidoptera	Geometridae	*Ematurga atomaria*	1	1	0.00	-0.0782
Lepidoptera	Geometridae	*Minoa murinata*	2	2	0.00	-0.1451
Lepidoptera	Geometridae	*Odezia atrata*	3	1	0.00	0.0695
Lepidoptera	Geometridae	*Rheumaptera cf. subhastata*	1	1	0.00	-0.0898
Lepidoptera	Hesperiidae	*Hesperia comma*	11	6	0.42	-0.1394
Lepidoptera	Hesperiidae	*Ochlodes sylvanus*	15	8	0.33	-0.1409
Lepidoptera	Hesperiidae	*Pyrgus malvae*	5	5	0.71	-0.1782
Lepidoptera	Hesperiidae	*Thymelicus lineola*	8	6	0.16	0.0528
Lepidoptera	Hesperiidae	*Thymelicus sylvestris*	76	19	0.44	-0.1252
Lepidoptera	Lycaenidae	*Callophrys rubi*	1	1	0.26	-0.1091
Lepidoptera	Lycaenidae	*Cupido minimus*	7	3	0.37	-0.0884
Lepidoptera	Lycaenidae	*Cyaniris semiargus*	15	10	0.48	-0.1371
Lepidoptera	Lycaenidae	*Lycaena hippothoe*	5	4	0.17	-0.1101

Lepidoptera	Lycaenidae	*Phengaris arion*	3	2	0.18	-0.0897
Lepidoptera	Lycaenidae	*Plebeius argus/argyrognomon/idas agg.*	87	16	0.38	-0.2974
Lepidoptera	Lycaenidae	*Polyommatus amandus*	3	2	0.11	-0.1323
Lepidoptera	Lycaenidae	*Polyommatus bellargus*	1	1	0.61	-0.1419
Lepidoptera	Lycaenidae	*Polyommatus coridon*	39	7	0.47	-0.1176
Lepidoptera	Lycaenidae	*Polyommatus icarus*	106	20	0.44	-0.0234
Lepidoptera	Lycaenidae	*Pseudophilotes baton*	1	1	0.53	-0.0994
Lepidoptera	Noctuidae	*Autographa gamma*	17	4	0.36	0.1154
Lepidoptera	Noctuidae	*Euclidia glyphica*	3	3	0.16	-0.0865
Lepidoptera	Noctuidae	*Panemeria tenebrata*	1	1	0.81	0.1390
Lepidoptera	Noctuidae	*Polyphaenis sericata*	1	1	0.00	-0.0386
Lepidoptera	Noctuidae	*Tyta luctuosa*	5	3	0.70	0.0084
Lepidoptera	Nymphalidae	*Aphantopus hyperantus*	18	10	0.15	-0.1052
Lepidoptera	Nymphalidae	*Argynnis adippe*	1	1	0.48	0.1072
Lepidoptera	Nymphalidae	*Argynnis aglaja*	1	1	0.00	0.1101
Lepidoptera	Nymphalidae	*Coenonympha arcania*	1	1	0.00	-0.1323
Lepidoptera	Nymphalidae	*Coenonympha glycerion*	1	1	0.00	-0.1207
Lepidoptera	Nymphalidae	*Coenonympha pamphilus*	52	16	0.37	-0.0477
Lepidoptera	Nymphalidae	*Erebia medusa*	5	1	0.00	-0.0666
Lepidoptera	Nymphalidae	*Inachis io*	16	6	0.04	0.0023
Lepidoptera	Nymphalidae	*Maniola jurtina*	55	19	0.26	-0.0356
Lepidoptera	Nymphalidae	*Melanargia galathea*	50	9	0.49	-0.1111
Lepidoptera	Nymphalidae	*Melitaea cf. aurelia*	1	1	0.00	-0.1419
Lepidoptera	Nymphalidae	*Melitaea cf. britomartis*	16	9	0.23	-0.3347
Lepidoptera	Papilionidae	*Papilio machaon*	5	2	0.52	-0.0959
Lepidoptera	Pieridae	*Colias cf. hyale*	2	2	0.50	-0.0936
Lepidoptera	Pieridae	*Gonepteryx rhamni*	1	1	0.11	0.1072
Lepidoptera	Pieridae	*Pieris brassicae*	30	8	0.30	0.0593
Lepidoptera	Pieridae	*Pieris napi*	2	2	0.00	0.0408
Lepidoptera	Pieridae	*Pieris rapae*	17	5	0.14	0.0965
Lepidoptera	Sphingidae	*Hemaris tityus*	1	1	0.00	-0.0666
Lepidoptera	Zygaenidae	*Zygaena cf. viciae*	2	2	0.30	-0.1361
Lepidoptera	Zygaenidae	*Zygaena filipendulae*	38	9	0.45	-0.2219
Lepidoptera	Zygaenidae	*Zygaena loti*	1	1	0.81	0.0183
Lepidoptera	Zygaenidae	*Zygaena purpuralis/minos agg.*	95	16	0.36	-0.2268

Table S3: Abundance, number of flower visitor species, specialisation (d_i') and land-use responses (mean r_S) of 166 flowering plant species.

Family	Species	Number of flowering units	Number of visitor species	Weighted mean d_i'	Mean land-use response (r_S)
Anthericaceae	*Anthericum ramosum*	1	1	1.00	-0.0772
Apiaceae	*Aegopodium podagraria*	142	33	0.65	0.1037
Apiaceae	*Anthriscus sylvestris*	1234	137	0.65	0.0968
Apiaceae	*Apiaceae undet.*	2	1	0.53	0.0763
Apiaceae	*Bunium bulbocastanum*	34	15	0.65	-0.1149
Apiaceae	*Carum carvi*	982	146	0.54	0.0857
Apiaceae	*Chaerophyllum aureum*	90	34	0.47	0.1078
Apiaceae	*Chaerophyllum bulbosum*	8	2	0.65	-0.1323
Apiaceae	*Chaerophyllum hirsutum*	7	5	1.00	0.0299
Apiaceae	*Chaerophyllum temulum*	6	3	0.58	-0.1149
Apiaceae	*Daucus carota*	1501	152	0.54	-0.1253
Apiaceae	*Falcaria vulgaris*	3	2	0.12	-0.0338
Apiaceae	*Heracleum sphondylium*	2374	227	0.62	0.3111
Apiaceae	*Pastinaca sativa*	335	70	0.54	-0.0094
Apiaceae	*Pimpinella major*	95	22	0.79	0.1564
Apiaceae	*Pimpinella saxifraga*	514	81	0.67	-0.1433
Apiaceae	*Silaum silaus*	35	25	0.70	-0.1431
Apiaceae	*Torilis japonica*	1	1	0.44	0.0150
Asteraceae	*Achillea millefolium*	2224	173	0.57	-0.0144
Asteraceae	*Antennaria dioica*	17	7	0.89	-0.0650
Asteraceae	*Anthemis arvensis*	27	13	0.78	-0.0290
Asteraceae	*Arctium tomentosum*	18	7	0.79	0.0041
Asteraceae	*Bellis perennis*	109	38	0.61	-0.0048
Asteraceae	*Buphthalmum salicifolium*	1	1	0.66	-0.1181
Asteraceae	*Carduus acanthoides*	1	1	0.36	-0.0747
Asteraceae	*Carduus crispus*	17	11	0.82	0.0032
Asteraceae	*Carduus nutans*	1	1	0.33	-0.0608
Asteraceae	*Carlina acaulis*	16	6	0.17	-0.0936
Asteraceae	*Carlina vulgaris*	1	1	0.00	-0.1091
Asteraceae	*Centaurea jacea*	188	37	0.70	-0.0721
Asteraceae	*Centaurea scabiosa*	5	5	0.73	-0.0962
Asteraceae	*Cichorium intybus*	26	16	0.26	-0.0687
Asteraceae	*Cirsium acaule*	35	9	0.56	-0.2372
Asteraceae	*Cirsium arvense*	236	83	0.58	0.0837
Asteraceae	*Cirsium eriophorum*	5	3	0.49	0.0913
Asteraceae	*Cirsium oleraceum*	230	28	0.60	0.1280
Asteraceae	*Cirsium palustre*	12	4	0.67	-0.0491
Asteraceae	*Cirsium vulgare*	62	18	0.56	-0.1316
Asteraceae	*Crepis biennis*	967	125	0.51	0.0998
Asteraceae	*Crepis capillaris*	10	4	0.32	0.1370
Asteraceae	*Crepis mollis*	30	15	0.55	-0.1043
Asteraceae	*Crepis tectorum*	8	4	0.42	-0.0088
Asteraceae	*Hieracium pilosella*	126	30	0.50	-0.3244
Asteraceae	*Hypochoeris radicata*	662	99	0.48	-0.0493
Asteraceae	*Leontodon autumnalis*	48	18	0.47	-0.1521
Asteraceae	*Leontodon hispidus*	406	71	0.54	-0.3602
Asteraceae	*Leucanthemum ircutianum*	327	90	0.62	-0.3704
Asteraceae	*Leucanthemum vulgare*	269	72	0.61	-0.1524

Asteraceae	*Picris hieracioides*	9	8	0.38	0.0362
Asteraceae	*Senecio erucifolius*	7	5	0.60	-0.1231
Asteraceae	*Senecio jacobaea*	44	24	0.50	-0.0209
Asteraceae	*Sonchus arvensis*	2	2	0.02	-0.0386
Asteraceae	*Taraxacum officinale*	785	134	0.61	0.1568
Asteraceae	*Tragopogon orientalis*	103	30	0.51	-0.0448
Asteraceae	*Tragopogon pratensis*	4	4	0.47	-0.0632
Asteraceae	*Tripleurospermum maritimum*	69	35	0.50	0.1247
Boraginaceae	*Myosotis arvensis*	6	2	0.21	0.1263
Boraginaceae	*Myosotis palustris*	4	3	0.59	-0.1207
Boraginaceae	*Symphytum officinale*	44	14	0.58	-0.0311
Brassicaceae	*Capsella bursa-pastoris*	12	10	0.44	0.1430
Brassicaceae	*Cardamine hirsuta*	3	3	0.07	0.0890
Brassicaceae	*Cardamine pratensis*	84	12	0.82	-0.0382
Brassicaceae	*Cardaminopsis arenosa*	34	10	0.32	0.0034
Brassicaceae	*Erysimum cheiranthoides*	37	12	0.48	0.1294
Brassicaceae	*Thlaspi arvense*	1	1	0.00	-0.1231
Campanulaceae	*Campanula patula*	14	8	0.76	0.0044
Campanulaceae	*Campanula rapunculoides*	1	1	0.40	-0.0082
Campanulaceae	*Campanula rotundifolia*	28	12	0.75	-0.2174
Caryophyllaceae	*Cerastium holosteoides*	124	29	0.55	0.2938
Caryophyllaceae	*Dianthus carthusianorum*	3	3	0.39	-0.2330
Caryophyllaceae	*Lychnis flos-cuculi*	2	2	0.13	-0.0912
Caryophyllaceae	*Silene armeria*	1	1	1.00	0.0956
Caryophyllaceae	*Silene dioica*	1	1	0.00	0.0217
Caryophyllaceae	*Stellaria graminea*	24	14	0.47	-0.0295
Caryophyllaceae	*Stellaria holostea*	1	1	0.55	0.0743
Caryophyllaceae	*Stellaria media*	7	5	0.36	0.0295
Caryophyllaceae	*Stellaria sp.*	1	1	0.36	-0.1207
Cistaceae	*Helianthemum nummularium*	75	22	0.50	-0.2390
Colchicaceae	*Colchicum autumnale*	15	3	0.83	-0.0146
Convolvulaceae	*Convolvulus arvensis*	652	62	0.62	-0.0135
Dipsacaceae	*Knautia arvensis*	74	17	0.76	-0.1470
Dipsacaceae	*Knautia dipsacifolia*	7	5	0.35	-0.0850
Dipsacaceae	*Scabiosa columbaria*	280	38	0.66	-0.2802
Euphorbiaceae	*Euphorbia cyparissias*	562	41	0.73	-0.1941
Fabaceae	*Anthyllis vulneraria*	74	24	0.59	-0.1395
Fabaceae	*Astragalus glycyphyllos*	8	3	0.48	-0.0705
Fabaceae	*Genista tinctoria*	5	4	0.55	-0.2070
Fabaceae	*Hippocrepis comosa*	48	9	0.85	-0.1166
Fabaceae	*Lathyrus pratensis*	6	4	0.42	-0.1083
Fabaceae	*Lotus corniculatus*	585	56	0.68	-0.3873
Fabaceae	*Medicago lupulina*	39	23	0.55	-0.2078
Fabaceae	*Medicago sativa*	105	8	0.80	0.2234
Fabaceae	*Trifolium arvense*	2	2	0.28	0.0270
Fabaceae	*Trifolium campestre*	5	4	0.67	-0.2210
Fabaceae	*Trifolium dubium*	6	5	0.53	-0.1013
Fabaceae	*Trifolium hybridum*	2	1	1.00	-0.0909
Fabaceae	*Trifolium medium*	79	17	0.59	-0.2557
Fabaceae	*Trifolium montanum*	8	6	0.29	-0.0993
Fabaceae	*Trifolium pratense*	850	69	0.67	0.1375
Fabaceae	*Trifolium repens*	2562	103	0.74	0.1469
Fabaceae	*Vicia angustifolia*	2	2	0.50	-0.1358
Fabaceae	*Vicia cracca*	32	11	0.62	-0.1549
Fabaceae	*Vicia sepium*	110	20	0.71	0.1499

Geraniaceae	*Erodium cicutarium*	1	1	1.00	-0.0582
Geraniaceae	*Geranium pratense*	39	14	0.52	0.0727
Geraniaceae	*Geranium pusillum*	1	1	0.60	0.1132
Geraniaceae	*Geranium pyrenaicum*	74	19	0.57	0.1269
Geraniaceae	*Geranium sylvaticum*	392	51	0.41	0.1105
Hypericaceae	*Hypericum maculatum*	9	8	0.50	0.0183
Hypericaceae	*Hypericum perforatum*	18	13	0.62	-0.3413
Hypericaceae	*Hypericum pulchrum*	3	3	0.55	-0.1187
Lamiaceae	*Ajuga genevensis*	1	1	0.27	-0.1711
Lamiaceae	*Betonica officinalis*	30	6	0.67	0.0010
Lamiaceae	*Glechoma hederacea*	7	5	0.86	-0.0477
Lamiaceae	*Lamium album*	49	9	0.61	0.2733
Lamiaceae	*Lamium purpureum*	18	5	0.80	-0.0907
Lamiaceae	*Mentha aquatica*	4	3	0.84	-0.0048
Lamiaceae	*Origanum vulgare*	10	6	0.48	-0.0474
Lamiaceae	*Prunella grandiflora*	189	30	0.57	-0.1773
Lamiaceae	*Prunella vulgaris*	15	8	0.51	-0.0913
Lamiaceae	*Salvia pratensis*	5	3	0.58	-0.1364
Lamiaceae	*Teucrium chamaedrys*	3	2	0.25	-0.1091
Lamiaceae	*Teucrium montanum*	36	8	0.53	-0.1935
Lamiaceae	*Thymus pulegioides*	216	40	0.49	-0.3498
Linaceae	*Linum cartharticum*	6	2	0.24	-0.3295
Onagraceae	*Epilobium parviflorum*	4	1	0.08	-0.0048
Plantaginaceae	*Plantago lanceolata*	105	27	0.62	0.0287
Plantaginaceae	*Plantago major*	4	1	0.93	0.0082
Plantaginaceae	*Plantago media*	319	45	0.56	-0.2001
Polygalaceae	*Polygala amara*	1	1	0.26	-0.2024
Polygalaceae	*Polygala comosa*	2	2	0.23	-0.2592
Polygonaceae	*Rumex obtusifolius*	2	2	1.00	0.0213
Ranunculaceae	*Caltha palustris*	1	1	0.79	-0.0365
Ranunculaceae	*Ranunculus acris*	782	132	0.58	0.1659
Ranunculaceae	*Ranunculus arvensis*	1	1	0.39	-0.1165
Ranunculaceae	*Ranunculus bulbosus*	259	51	0.54	-0.3035
Ranunculaceae	*Ranunculus nemorosus*	43	20	0.72	0.1187
Ranunculaceae	*Ranunculus repens*	695	103	0.53	0.0039
Ranunculaceae	*Ranunculus sceleratus*	6	5	0.30	-0.1323
Rosaceae	*Agrimonia eupatoria*	23	10	0.57	-0.2877
Rosaceae	*Alchemilla vulgaris*	1	1	1.00	0.0395
Rosaceae	*Potentilla anserina*	70	31	0.57	0.0008
Rosaceae	*Potentilla argentea*	14	4	0.60	-0.0016
Rosaceae	*Potentilla erecta*	27	12	0.40	-0.0902
Rosaceae	*Potentilla reptans*	199	52	0.45	0.0023
Rosaceae	*Potentilla verna*	5	5	1.00	-0.0615
Rosaceae	*Rosa canina*	15	10	0.64	-0.2454
Rosaceae	*Rosa rubiginosa*	7	6	0.72	-0.1390
Rosaceae	*Rubus idaeus*	1	1	0.17	-0.0392
Rubiaceae	*Asperula cynanchica*	18	9	0.34	-0.2158
Rubiaceae	*Galium aparine*	1	1	0.27	-0.0126
Rubiaceae	*Galium mollugo agg.*	342	80	0.56	-0.0368
Rubiaceae	*Galium pumilum*	13	5	0.45	-0.2444
Rubiaceae	*Galium verum*	20	9	0.41	-0.3395
Scrophulariaceae	*Euphrasia officinalis*	13	5	0.75	-0.2790
Scrophulariaceae	*Odontites vulgaris*	60	8	0.84	-0.0427
Scrophulariaceae	*Rhinanthus alectorolophus*	8	5	0.60	-0.1195
Scrophulariaceae	*Rhinanthus angustifolius*	15	8	0.43	-0.0575

Scrophulariaceae	*Rhinanthus major*	11	8	0.63	0.0010
Scrophulariaceae	*Rhinanthus minor*	14	9	0.75	-0.1651
Scrophulariaceae	*Veronica anagallis-aquatica*	2	1	0.18	0.1294
Scrophulariaceae	*Veronica arvensis*	1	1	0.36	0.0912
Scrophulariaceae	*Veronica chamaedrys*	69	16	0.57	-0.0303
Scrophulariaceae	*Veronica officinalis*	1	1	0.24	-0.1265
Scrophulariaceae	*Veronica persica*	2	2	0.60	0.0708
Scrophulariaceae	*Veronica teucrium*	2	2	1.00	-0.0831

4. Differences in land-use effects on plant-pollinator interaction across three different German bioregions

This chapter is in preparation as:
Weiner, C.N., Werner, M., Linsenmair, K.-E., Blüthgen, N.: ***Land-use intensification triggers diversity loss in pollination networks: Regional distinctions between three different German bioregions***

Summary

Agricultural intensification may pose a serious risk to biodiversity preservation and ecosystem services such as pollination. On 119 grassland sites in three German bioregions differing in climate and geology we documented plant-pollinator interactions along a gradient of increasing land-use intensity. We analyzed abundance, diversity, composition and specialization focusing on the isolated effects of fertilization, mowing and grazing intensity.

We found strong regional differences in plant as well as in pollinator response to land-use intensity and its isolated compounds. Yet, throughout the regions, pollinator fate was determined by the average land-use response of the plant species they visited and vice versa. Moreover, in pollinators – but not in plants – land-use intensification disproportionately affected specialized species.

These results show how closely plants and pollinators rely on each other and that a decline in plant species might have rigorous consequences for their visitors. We demonstrate that it is not advisable to transfer results and management recommendations readily from one region to another. Regional conditions have to be carefully analyzed before reasoning on how a system will react to land-use changes. Neither plants nor pollinators react the same way to management conditions under a different regional context.

4.1 Introduction

Understanding the relationship between ecosystem functioning and human-induced changes in biodiversity via land-use has become a major challenge for scientists worldwide. Despite the explosion of research that has taken place on the topic, many uncertainties remain (Hooper et al. 2005). Thus, further inside to the relationship

between land-use and taxonomic as well as functional diversity is essential for understanding the mechanisms by which biodiversity and gradual losses thereof may affect ecosystem functions and services (Loreau et al. 2001, Dunne et al. 2002, Kaiser-Bunbury et al. 2010).

Pollination is an important ecosystem service and it is considered at risk (Daily 1997, Klein et al. 2007, Aizen and Harder 2009). Agricultural intensification triggers losses in the diversity of plant and pollinator communities via habitat conversion (Keitt 2009), fragmentation (Rathcke and Jules 1993), fertilization (Burkle and Irwin 2010), mowing and grazing (Gibson et al. 1992, Kruess and Tscharntke 2002, Socher et al. 2013) as well as pesticide use (Desneux et al. 2007). While in line with the intermediate disturbance hypothesis light grazing or mowing regimes can also augment species richness and enhance diversity of grasslands (Collins et al. 1998), heavy grazing or mowing considerably alters species composition and reduces plant diversity (Kruess and Tscharntke 2002, Zechmeister et al. 2003, Mayer 2004). Also seed set is reduced in heavily grazed grasslands due to diversity reductions in pollinators (Mayer 2004). Concerning pollinators, land-use intensification, e.g. increased mowing frequency, may have direct effects on pollinator diversity and abundance via disruption of life cycles (Johst et al. 2006) and indirect effects via resource availability. However, different insect species show differences in their response to agricultural management (Sjödin et al. 2008). There is evidence that pollinator species response to land-use may be also determined by pollinator specialization and interaction strength (Weiner et al. 2014). Especially in specialized species their land-use response and the mean land-use response of flowers visited are expected to be positively correlated, if plants determine the response of visitors and vice versa.

Regarding the preservation of ecosystem functions and services, management decisions have to be made which agricultural practices are appropriate to sustain the ecosystem service of pollination and which management regimes encourage the species most important to this service. In such cases species richness or diversity may not always be the best measures to describe ongoing changes, as another source of biodiversity loss – biological homogenization – may easily be overlooked (Filippi-Codaccioni et al. 2010).

In the present study, we compare abundance, diversity, composition and specialization of quantitative pollination networks across three different German bioregions and along

a continuous gradient of increasing land-use intensity. We examine which components of land-use (mowing, grazing, fertilization) most fundamentally influence herbal species richness and abundance as well as species richness, abundance and composition of pollinators. Moreover, we take a closer look at specialization of plant-pollinator interactions and its possible influence in relation to species loss.

We expect that (i) individual land-use components have marked effects on species richness, abundance and composition of plant-pollinator associations and that (ii) the direction in which different land-use practices influence diversity and abundance vary between pollinator groups. Yet, (iii) across regions we expect that responses of plants and pollinators to land-use are also determined by species specialization and the average land-use response of their interaction partners.

4.2 Methods

4.2.1 Study area and land-use gradient

We studied a variety of differently used grasslands in three major German research areas, the so-called Biodiversity Exploratories (Fischer et al. 2010). These Exploratories are located in the Schorfheide-Chorin (NE Germany), Hainich-Dün (Central Germany) and Schwäbische Alb (SW Germany) region. Each Exploratory covers an area of 422 - 1300 km² of land and comprises 50 experimental grassland plots measuring 50 × 50 m each. The plots are situated within a matrix of agricultural land in use and are managed accordingly by their owners. Fischer et al. (2010) give a detailed description of all plot selection criteria. Represented land-use types range from near-natural, protected sites to intensively fertilized, mown or grazed meadows and pastures (sheep, horses, cattle).

As purely qualitative categorization of land-use types disregards quantitative variations in intensity within a category, we used a quantitative land-use index (L) on a continuous scale, which incorporates fertilization (kg N × ha^{-1} × $year^{-1}$), mowing (mowing frequency × $year^{-1}$) and grazing intensity (livestock units × days × ha^{-1} × $year^{-1}$).

For each plot *k* the land-use intensity L_k is defined as the square root of the sum of the contributing land-use variables, divided by the respective mean of the variable over all 150 sites (“global” standardization):

$$L_k = \sqrt{\frac{G_k}{G_{mean}} + \frac{F_k}{F_{mean}} + \frac{M_k}{M_{mean}}}$$

Due to the standardization by ratios, L_k is dimensionless. To examine how land-use intensity influences plant-pollinator communities and to determine the isolated effects of fertilization, mowing and grazing, we used linear models and the mean L_k of the years (2006 - 2008) or the raw values for fertilization, mowing and grazing intensity. A former version of land-use index used here has been shown to predict responses in plant and pollinator diversity in former studies (Blüthgen et al. 2012, Weiner et al. 2014). All 119 sites investigated were in use by land owners between 2006 and 2008. Nevertheless, 69 of these plots had not been fertilized, 46 had not been mown and 28 had not been grazed during this three-year-period. While fertilization and mowing intensities were correlated positively across all investigated plots, grazing and fertilization as well as grazing and mowing intensities were negatively correlated (Figure 7). The absence of grazing thus often corresponds to frequent mowing and heavy fertilization while grazed sites are usually not fertilized and not or rarely mown.

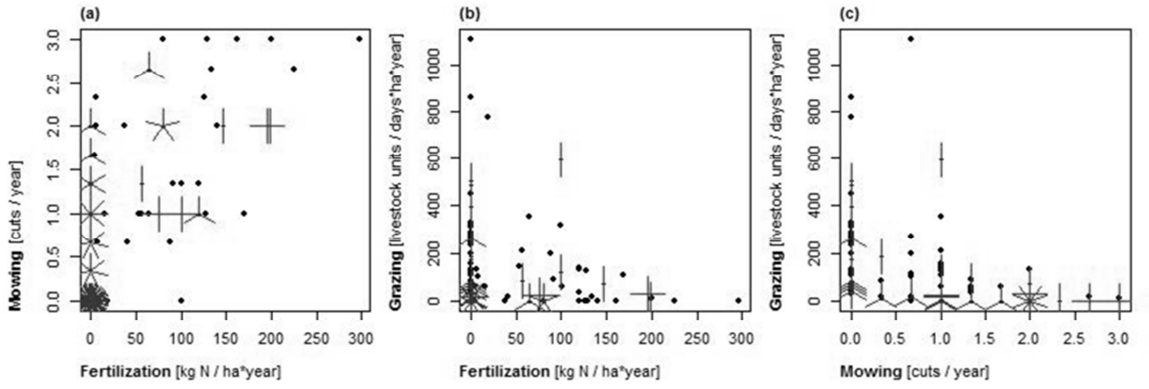

Figure 7: Relationship between the land-use components fertilization, mowing and grazing intensity. Spearman rank correlations for (a) $r_s = 0.68$, (b) $r_s = -0.22$, (c) $r_s = -0.64$, all $p > 0.01$. The number of lines around the point indicates overlapping data (starplots).

4.2.2 Data collection

During peak flowering 2008 (May to August) we conducted 162 surveys (Alb: 63; Hainich: 51; Schorfheide: 48) and studied plant-pollinator interactions on 119 experimental grassland plots, sampling 29 plots repeatedly up to four times. 31 of the 150 experimental plots could not be sampled because there were no flowering plants at the time of visit, mainly due to grazing or mowing. Each survey covered a transect area

measuring 200 × 3 m (length × width) and six hours of sampling between morning and afternoon with the 200 m intercept being sampled three times and yielded a single interaction network, which we analyzed separately. To avoid pseudo-replication we calculated the mean value per plot and variable for surveys on plots which were sampled repeatedly two to three times within 30 days. This pertained to 27 surveys on 13 plots in the Alb and resulted in n = 49 surveys in the Alb. We consider our analyses of land-use effects as unbiased by spatial and temporal effects, as Mantel tests based on Bray-Curtis distance and 10^5 permutations showed no correlations between spatial arrangement of the plots and species composition and land-use intensity was not correlated with sampling date or spatial distance in any Exploratory (see Chapter 3; Weiner et al. 2014).

We exclusively recorded visitors that touched the reproductive parts of a flower – thus likely to be pollinators - , as well as the plant species they visited. Specimens that could not be identified in the field were collected and later identified to species level by experts (see acknowledgements). We analyzed flower visits from insect visitors belonging to the orders of hymenoptera, lepidoptera, diptera and coleoptera. However, Nitidulidae (sap beetles) were excluded from our analysis as they are easily overlooked or under-sampled in structurally complex flowers, which may create a bias for some plants if collected erratically.

To account for flower abundance per plant species and transect we counted the number of flowering units (a unit refers to one or more flowers demanding an insect to fly in order to reach the next unit) or, in highly abundant species, extrapolated it from a small area. Flower diversity was assessed by multiplying the number of flowering units per species by its average flowering area in cm^2, to account for differences in flowering area, which are related to pollinator attraction (Grindeland et al. 2005). A detailed description of measurement of flowering area is given in Weiner et al. (2011).

4.2.3 Response variables

To test effects land-use intensity and its individual components have on plant-pollinator associations, we choose three types of response variables: diversity, abundance and compositional variables. These variables are assumed to be suitable to test land-use effects because we expect direct or indirect responses to more intensive land-use. For

example plant diversity is known to respond negatively to intensive mowing (Zechmeister et al. 2003), while pollinator diversity and abundance is reduced on overgrazed pastures (Mayer 2004) and shifts in insect species composition have been observed in relation to fertilization and subsequent changes in plant species composition (Haddad et al. 2000).

For each independent survey response variables were calculated separately for plants and pollinators as well as for six pollinator groups, namely bees, other hymenopterans, syrphids, other flies, butterflies and beetles. Bees were segregated from other hymenopterans and syrphids from other flies as because both are commonly used bioindicator taxa (Jauker et al. 2009).

We used species richness and alternatively the exponential of the Shannon index (e^H) to estimate diversity. Results on the latter are given in the appendix (Table A1). Abundance was defined as total flower area per plot in plants, while in pollinators it was defined as total number of pollinator individuals or number of individuals from a pollinator group per plot, respectively. Pollinator composition was calculated as relative abundance per pollinator group and experimental plot.

To gain information on the German Red List status of all pollinator species identified, we surveyed literature (Binot et al. 1998, Binot-Hafke et al. 2011) and assigned a red list status to each pollinator subsequently, or, in species not listed, the status "data deficient". For later analysis, all species assigned as *vulnerable*, *extremely rare*, *endangered, critically endangered* or *near extinction* were categorized as *threatened*, all species known to be not endangered as *not threatened* and all other species as *data deficient*.

4.2.4 Statistical analysis

To assess the relationship between the response variables and the LUI index or its individual components (fertilization, mowing, grazing) respectively, we used linear regressions:

$y = a \cdot x + b$, where a is the slope and b the intercept

These were calculated for each response variable in each of the three Exploratories separately.

We computed the mean square error (RMSE) for each model and Exploratory and assessed model significance with an F-test. Moreover, as a rough goodness-of-fit measure, we computed squared Pearson correlation coefficients between observed and fitted values (R^2-values).

Network and species specialization of plants and flower visitors were calculated using the information-theoretical specialization metrics H_2' and d' derived from the Kullback–Leibler distance (Blüthgen et al. 2006). H_2' discloses the degree of niche complementarity within a network, whereas d' in our case describes a species' deviation in flower visitation from the distribution of all flower visitors. Both metrics range from zero to one with high values indicating more pronounced specialization. Due to a null-model-based correction, the indices are unaffected by variation in sampling effort or total interaction frequency (Blüthgen et al. 2007).

To identify the general land-use response of a species, for each species i we calculated Spearman correlation coefficients (r_s) of relative species abundance (per cent of total individuals) per plot and land-use intensity in each Exploratory. Actual species response to land-use may relate to both, species specialization and the average land-use responses of the specific partners a species depends on. If so, the identity and interaction strength of links within a network gives a hint on how species respond to diversity changes. We calculated the weighted mean d_i' (weighted by a species i total interactions per Exploratory and plot k) of each species to test for a relationship between species specialization and land-use response. Furthermore, for pollinators we determined the weighted mean land-use response of all specific partner plants frequented by pollinator species i (E_i), weighted by the number of interactions a_{ij} between a pollinator species i and its specific partner plants j. For plants we determined the weighted mean land-use response of all specific flower visitors of a plant j (E_j), also weighted by the number of

interactions a_{ij} between a plant species *j* and its specific pollinators *i*. We used ANCOVA (type II SS) to test the determinants of a species´ land-use response (r_{is}) including E_i and d_i' in the model as predictors for pollinator response and E_j and d_j' as predictors for plant response. All calculations followed the methods described at full length in Chapter 3 (see Weiner et al. 2014).

We conducted all statistical analyses in R 3.1.3 (R Development Core Team 2015). Calculations of H_2' and *d*' were made with the function dfun in the package 'bipartite' (Dormann et al. 2009).

4.3 Results

4.3.1 Land-use effects on plant communities

Overall, we recorded 249 plant species from 32 families, with the highest species richness occurring in the Schwäbische Alb (163 species), followed by the Hainich (143) and the Schorfheide Exploratory (106). Also the mean diversity per plot was highest in the Alb (5.63 ± 2.89), followed by the Hainich (4.86 ± 2.56) and the Schorfheide Exploratory (2.97 ± 1.75). While overall flowering area per site did not respond significantly to land-use intensity in either of the Exploratories (Table 7, Figure 8), plant species richness declined with increasing land-use intensity in the Alb and Hainich, but not in the Schorfheide Exploratory (Table 7, Figure 8). In the Alb and Hainich Exploratories plant species richness decreased with increasing fertilizer input. Moreover, an increase in mowing frequency went along with a negative trend in plant species richness, but significant effects occurred in the Alb Exploratory only (Table 7). Grazing had a positive effect on species richness in the Alb Exploratory (Table 7, Figure 8).

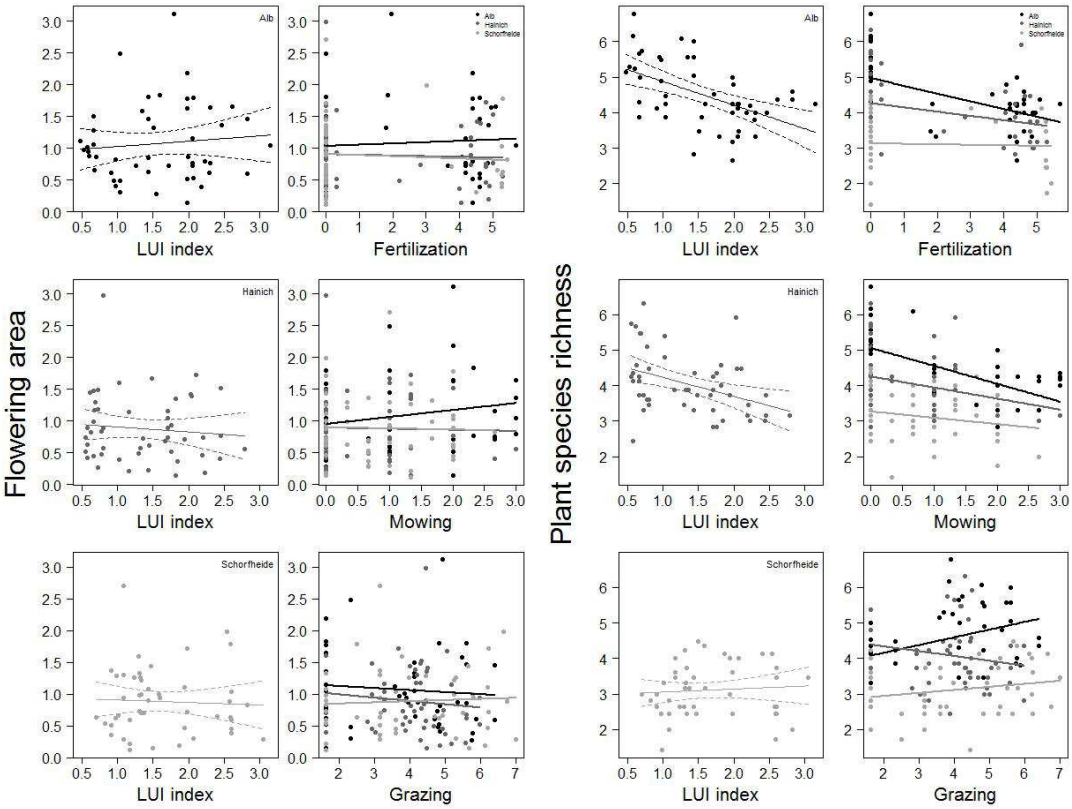

Figure 8: Relationship between flowering area (left) respectively plant species richness (right) and land-use intensity (LUI, left panels) and its individual components (right panels).

4.3.2 Land-use effects on red list species and pollinator communities

We identified a total of 741 pollinator species, with 463 species found in the Alb, 403 in the Hainich and 332 in the Schorfheide Exploratory. We recorded 115 bee species, 48 other hymenopterans, 50 butterflies, 104 beetles, 103 syrphids and 321 other dipteran species. 94 species were classified as *threatened* (see methods), 355 species as *not threatened* and 292 species as *data deficient*. Species richness of threatened pollinator species responded negatively in the Alb (Figure 9). Here an increase in fertilization was associated with decreasing species richness of threatened pollinator species (Table 6). Absolute abundance of *threatened* pollinators was correlated positively to land-use intensity in the Schorfheide Exploratory (Figure 9). None of the individual LUI components had significant effects on the absolute abundance of threatened pollinator individuals in any Exploratory (Table 6).

Table 6: Univariate relationships between land-use intensity (LUI), as well as its individual components and response variables.

Response variable	Region	N	LUI index			Fertilization intensity			Mowing intensity			Grazing intensity		
			R^2	RMSE	*p*	R^2	RMSE	*p*	R^2	RMSE	*p*	R^2	RMSE	*p*
Richness of red list species	Alb	49	0,11	0,51	**0,02692**	0,14	0,50	**0,01028**	0,03	0,53	0,24826	0,00	0,54	0,88931
	Hainich	51	0,02	0,73	0,32665	0,00	0,74	0,88530	0,00	0,74	0,76316	0,01	0,73	0,47831
	Schorf-heide	48	0,03	0,60	0,27697	0,01	0,60	0,53445	0,00	0,61	0,76881	0,02	0,60	0,45775
Absolute abundance of red list Individuals	Alb	49	0,02	1,61	0,31934	0,03	1,61	0,26269	0,01	1,62	0,54941	0,00	1,63	0,80379
	Hainich	51	0,06	1,87	0,10742	0,01	1,91	0,53382	0,02	1,90	0,36040	0,00	1,92	0,69505
	Schorf-heide	48	0,11	1,74	**0,03838**	0,05	1,80	0,17257	0,04	1,81	0,22207	0,00	1,85	0,90551

Model fit is expressed as Pearson correlation coefficient (R^2) and root mean square error (RMSE), in addition to significance level (*p*). Significant fit ($p < 0.05$) was marked boldface. Additionally, positive correlations are highlighted in light grey, negative ones in dark grey. Number of sites (N) is shown for each response.

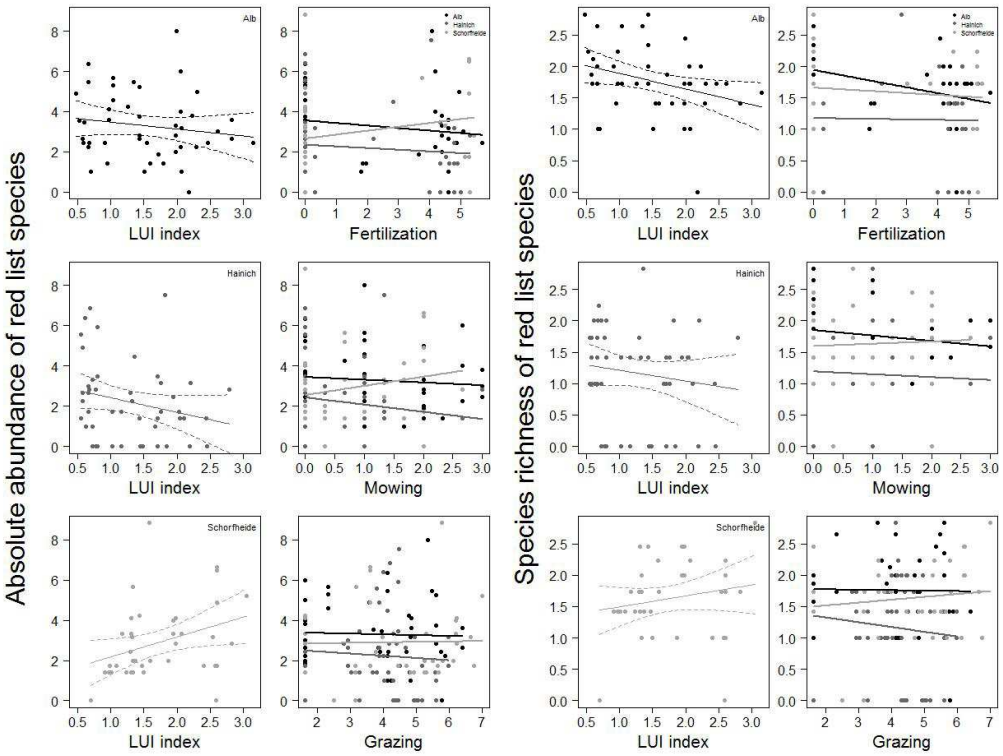

Figure 9: Relationship between the abundance of threatened pollinator species (left) as well as their species richness (right) and land-use intensity (LUI, left panels) and its individual components (right panels).

More detailed analysis of pollinator responses revealed opposing trends for different pollinator groups and different trends between the Exploratories (Table 7, Figure 10 - 16), which impedes the deduction of general implications for pollinator protection. Below results are ordered by Exploratory.

Schwäbische Alb: Overall pollinator abundance and species richness increased with increasing land-use intensity. An increase mowing frequency was accompanied by rising pollinator abundance, while species richness responded positive to both, fertilization and mowing (Table 7, Figure 10). However, we observed declines in species richness, absolute and relative abundance of butterflies in relation to land-use intensification as well as a strong negative trend in the species richness of bees. Simultaneously, species richness and absolute abundance of syrphids and in case of other flies additionally relative abundance increased (Table 7, Figure 11, 13, 15, 16). Thus we found compositional changes in the pollinator community towards more dipteran and less lepidopteran species with increasing land-use intensity.

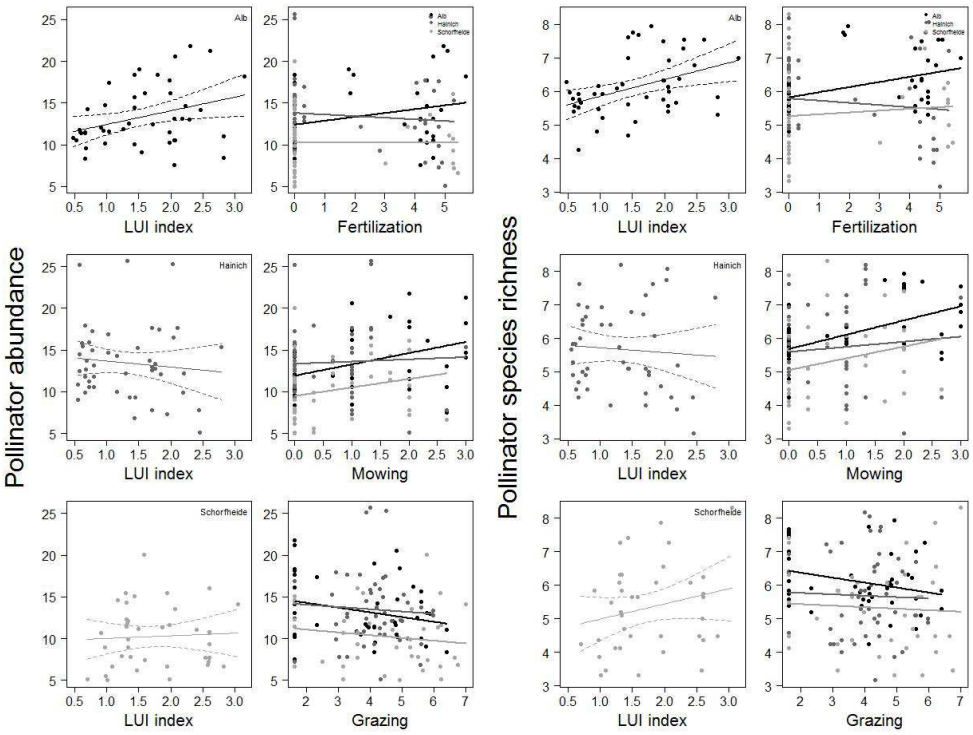

Figure 10: Relationship between pollinator abundance (left) respectively pollinator species richness (right) and land-use intensity (LUI, left panels) and its individual components (right panels).

Disentangling the land-use responses, we observed that with increases in fertilization and mowing the richness and abundance of butterflies decreased. The relationship was more distinct for fertilization than for mowing. In contrast, fertilization was positively related to richness of syrphids as well as to richness and abundances of other dipterans. Mowing intensity was positively correlated with richness and absolute abundance of

syrphids as well as with richness and abundances of other flies. In this case, we observed stronger positive effects from mowing than from fertilization. None of the pollinator groups showed a significant response to grazing intensity (Table 7).

Hainich: Neither overall pollinator abundance nor richness responded significantly to the LUI or one of its components (Table 7, Figure 10). Species richness of beetles, hymenopterans (excl. bees) and butterflies decreased with increasing land-use intensity. Hymenopterans and butterflies also decreased in abundance (absolute and relative). None of the pollinator groups responded positively to land-use intensification (Table 7, Figure 11 - 16). The LUI was a better predictor for pollinator response to land-use than the individual LUI components. Nevertheless, increases in fertilization were related to decreases in species richness of beetles as well as to decreases in the relative abundance of butterflies and a strong negative trend in their absolute abundance (Figure 13 and 14). Moreover, the intensification of mowing also went along with decreasing relative abundance of hymenopterans (excl. bees) and lower species numbers of beetles, though the effect was less distinct than in fertilization. Increases in grazing were related positively to species richness of beetles (Table 7, Figure 12 and 14).

Schorfheide: Neither overall pollinator abundance nor richness responded significantly to changes in land-use intensity (Table 7, Figure 10). Partially opposing the trends in the other Exploratories we found a positive response to land-use intensification in relative abundance of bees and butterflies and a strong positive trend in the species richness of bees, whereas the relative abundance of flies decreased with increasing land-use intensity (Table 7, Figure 11, 12, 16). Scrutinizing the responses of the individual LUI components we found that in syrphids higher fertilization went along with increasing relative abundance, but higher mowing frequency had an even more pronounced positive effect. An increase in mowing frequency went along with an increase of species richness, absolute and relative abundance of syrphids (Table 7, Figure 15), while species richness, and abundances of hymenopterans responded negatively (Figure 12). Increases in grazing intensity were associated with increases in the relative abundance of bees and butterflies. In trend the relative abundance of flies decreased (Figure 11, 13, 16).

Table 7: Univariate relationships between response variables and land-use intensity (LUI) or its individual components

Response variable	Exploratory	N	LUI index			Fertilization intensity			Mowing intensity			Grazing intensity		
			R^2	RMSE	p	R^2	RMSE	p	R^2	RMSE	p	R^2	RMSE	p
Plant species richness	Alb	49	0,26	0,78	**0,00017**	0,28	0,77	**0,00010**	0,36	0,73	**0,00001**	0,16	0,84	**0,00510**
	Hainich	51	0,15	0,79	**0,00428**	0,09	0,82	**0,03083**	0,07	0,83	0,05972	0,02	0,85	0,27727
	Schorfheide	48	0,01	0,71	0,61100	0,00	0,72	0,78074	0,04	0,70	0,18676	0,04	0,70	0,16891
Flowering area	Alb	49	0,01	0,60	0,50376	0,01	0,60	0,61762	0,04	0,59	0,17552	0,01	0,60	0,54918
	Hainich	51	0,01	0,52	0,50088	0,00	0,52	0,75950	0,00	0,52	0,86417	0,01	0,52	0,48903
	Schorfheide	48	0,00	0,52	0,75165	0,01	0,52	0,62538	0,00	0,52	0,85241	0,00	0,52	0,69060
Pollinator species richness	Alb	49	0,16	0,80	**0,00545**	0,15	0,81	**0,00899**	0,27	0,75	**0,00018**	0,08	0,84	0,06494
	Hainich	51	0,01	1,22	0,62540	0,01	1,22	0,44669	0,01	1,22	0,54272	0,00	1,23	0,81659
	Schorfheide	48	0,05	1,25	0,18129	0,01	1,28	0,58972	0,05	1,25	0,17737	0,00	1,28	0,72943
Pollinator abundance	Alb	49	0,11	3,33	**0,02538**	0,08	3,38	0,05358	0,17	3,21	**0,00430**	0,07	3,40	0,08033
	Hainich	51	0,01	4,33	0,48140	0,01	4,34	0,53192	0,00	4,35	0,76783	0,00	4,35	0,67043
	Schorfheide	48	0,00	3,63	0,74606	0,00	3,63	0,96336	0,05	3,54	0,16441	0,02	3,59	0,36552
Bee species richness	Alb	49	0,07	0,67	0,08466	0,03	0,68	0,22658	0,03	0,68	0,27038	0,00	0,69	0,76871
	Hainich	51	0,00	0,79	0,85600	0,00	0,79	0,91691	0,01	0,79	0,40899	0,00	0,79	0,66157
	Schorfheide	48	0,08	0,87	0,07758	0,00	0,90	0,87336	0,00	0,90	0,75525	0,02	0,89	0,38234
Bee abundance	Alb	49	0,00	3,10	0,81177	0,00	3,10	0,87071	0,02	3,07	0,38446	0,08	2,97	0,05674
	Hainich	51	0,01	3,22	0,49642	0,02	3,20	0,31252	0,01	3,22	0,57935	0,00	3,23	0,89139
	Schorfheide	48	0,02	3,54	0,34855	0,00	3,58	0,95846	0,00	3,58	0,85559	0,01	3,57	0,67197
Bee abundance (%)	Alb	49	0,05	0,26	0,11454	0,03	0,26	0,26388	0,01	0,26	0,61897	0,03	0,26	0,26962
	Hainich	51	0,00	0,31	0,78328	0,00	0,31	0,65605	0,00	0,31	0,95895	0,00	0,31	0,79628
	Schorfheide	48	0,12	0,29	**0,01755**	0,01	0,31	0,48070	0,03	0,31	0,25048	0,13	0,29	**0,01288**
Hymenopteran species richness	Alb	49	0,01	0,69	0,48330	0,03	0,68	0,23953	0,04	0,68	0,17565	0,02	0,68	0,31924
	Hainich	51	0,09	0,61	**0,04220**	0,07	0,61	0,06597	0,03	0,62	0,21491	0,00	0,63	0,75757
	Schorfheide	48	0,00	0,64	0,94049	0,01	0,64	0,52641	0,03	0,63	0,28650	0,03	0,63	0,26900
Hymenopteran abundance	Alb	49	0,00	2,23	0,68486	0,03	2,20	0,25106	0,03	2,20	0,22038	0,04	2,19	0,18948
	Hainich	51	0,09	3,20	**0,04391**	0,07	3,23	0,07837	0,06	3,23	0,08075	0,00	3,34	0,83240
	Schorfheide	48	0,04	1,37	0,25867	0,05	1,36	0,18934	0,11	1,31	**0,03925**	0,06	1,35	0,14835
Hymenopteran abundance (%)	Alb	49	0,01	0,19	0,41117	0,04	0,18	0,18251	0,05	0,18	0,10692	0,04	0,18	0,15644
	Hainich	51	0,09	0,26	**0,03624**	0,07	0,26	0,05551	0,08	0,26	**0,04667**	0,00	0,27	0,94481
	Schorfheide	48	0,04	0,19	0,17684	0,04	0,20	0,20180	0,16	0,18	**0,00426**	0,07	0,19	0,06433
Butterfly species richness	Alb	49	0,30	0,66	**0,00007**	0,28	0,67	**0,00018**	0,25	0,68	**0,00038**	0,06	0,77	0,11333
	Hainich	51	0,10	0,79	**0,02644**	0,06	0,81	0,10645	0,00	0,83	0,63390	0,04	0,81	0,16390
	Schorfheide	48	0,02	0,75	0,44399	0,01	0,76	0,56658	0,00	0,76	0,83225	0,02	0,75	0,37531
Butterfly abundance	Alb	49	0,23	1,51	**0,00071**	0,22	1,52	**0,00089**	0,18	1,56	**0,00315**	0,03	1,70	0,28471
	Hainich	51	0,12	1,59	**0,01624**	0,08	1,63	0,05589	0,01	1,69	0,53017	0,04	1,67	0,18965
	Schorfheide	48	0,00	1,19	0,71480	0,02	1,17	0,34943	0,00	1,19	0,90958	0,01	1,18	0,49893
Butterfly abundance (%)	Alb	49	0,34	0,12	**0,00001**	0,32	0,12	**0,00003**	0,30	0,12	**0,00004**	0,07	0,14	0,07491
	Hainich	51	0,15	0,12	**0,00524**	0,09	0,13	**0,02868**	0,04	0,13	0,18318	0,03	0,13	0,24673
	Schorfheide	48	0,04	0,09	0,16090	0,00	0,09	0,69968	0,03	0,09	0,27500	0,11	0,09	**0,02223**
Beetle species richness	Alb	49	0,00	0,88	0,98456	0,02	0,88	0,41238	0,00	0,88	0,64650	0,00	0,88	0,87399
	Hainich	51	0,10	0,62	0,02974	0,15	0,60	**0,00640**	0,13	0,61	**0,01061**	0,11	0,61	**0,01889**
	Schorfheide	48	0,01	0,84	0,59678	0,00	0,85	0,74163	0,03	0,83	0,26461	0,03	0,84	0,32879
Beetle abundance	Alb	49	0,00	2,46	0,80154	0,01	2,45	0,60816	0,01	2,45	0,60079	0,01	2,45	0,63159
	Hainich	51	0,01	2,21	0,50321	0,01	2,21	0,46674	0,00	2,22	0,88976	0,00	2,22	0,77544
	Schorfheide	48	0,01	1,69	0,59515	0,01	1,69	0,59682	0,07	1,63	0,10634	0,02	1,67	0,34354
Beetle abundance (%)	Alb	49	0,03	0,18	0,26839	0,00	0,19	0,65798	0,05	0,18	0,12570	0,00	0,19	0,71128
	Hainich	51	0,00	0,21	0,68331	0,00	0,21	0,80015	0,00	0,21	0,70521	0,01	0,21	0,39830
	Schorfheide	48	0,01	0,20	0,62120	0,00	0,20	0,87437	0,01	0,20	0,42597	0,02	0,20	0,30677
Syrphid species richness	Alb	49	0,16	0,63	**0,00555**	0,14	0,64	**0,01013**	0,26	0,59	**0,00033**	0,07	0,67	0,08611
	Hainich	51	0,02	0,78	0,34212	0,00	0,79	0,88429	0,05	0,77	0,13715	0,00	0,79	0,79711
	Schorfheide	48	0,01	0,97	0,47576	0,02	0,97	0,43312	0,12	0,92	**0,03248**	0,05	0,95	0,17313
Syrphid abundance	Alb	49	0,08	2,32	**0,04954**	0,07	2,34	0,08363	0,13	2,26	**0,01458**	0,02	2,40	0,40554
	Hainich	51	0,00	2,96	0,69092	0,00	2,96	0,85671	0,04	2,90	0,17592	0,00	2,96	0,76131
	Schorfheide	48	0,03	2,79	0,27211	0,04	2,78	0,21994	0,15	2,62	**0,01531**	0,05	2,77	0,17957
Syrphid abundance (%)	Alb	49	0,01	0,21	0,55388	0,00	0,21	0,67959	0,00	0,21	0,74194	0,01	0,21	0,53751
	Hainich	51	0,03	0,17	0,20531	0,01	0,17	0,41634	0,05	0,16	0,10145	0,00	0,17	0,68679
	Schorfheide	48	0,03	0,21	0,20714	0,08	0,21	**0,04797**	0,11	0,21	**0,02002**	0,02	0,22	0,32447
Fly species richness	Alb	49	0,27	1,12	**0,00019**	0,20	1,18	**0,00164**	0,33	1,08	**0,00003**	0,06	1,28	0,10497
	Hainich	51	0,00	1,41	0,66472	0,00	1,41	0,66983	0,00	1,41	0,75263	0,01	1,40	0,53752
	Schorfheide	48	0,03	0,81	0,27119	0,04	0,80	0,23719	0,03	0,81	0,32417	0,00	0,82	0,80711

Fly abundance	Alb	49	0,17	3,91	**0,00382**	0,14	3,98	**0,00909**	0,19	3,87	**0,00254**	0,04	4,21	0,17777
	Hainich	51	0,00	5,09	0,86451	0,00	5,08	0,63669	0,00	5,08	0,75409	0,00	5,09	0,83321
	Schorfheide	48	0,01	2,40	0,51472	0,01	2,41	0,59753	0,02	2,39	0,35201	0,04	2,37	0,25219
Fly abundance (%)	Alb	49	0,15	0,24	**0,00533**	0,12	0,24	**0,01624**	0,11	0,24	**0,01737**	0,01	0,26	0,53435
	Hainich	51	0,00	0,32	0,78970	0,00	0,32	0,96856	0,00	0,32	0,91999	0,00	0,32	0,91592
	Schorfheide	48	0,09	0,25	**0,03374**	0,03	0,26	0,24304	0,00	0,26	0,82048	0,07	0,25	0,06228

Model fit is expressed as Pearson correlation coefficient (R^2) and root mean square error (RMSE), in addition to significance level (p). Significant fit ($p < 0.05$) was marked boldface. Additionally, positive correlations are highlighted in light grey, negative ones in dark grey. Number of sites (N) is shown for each response.

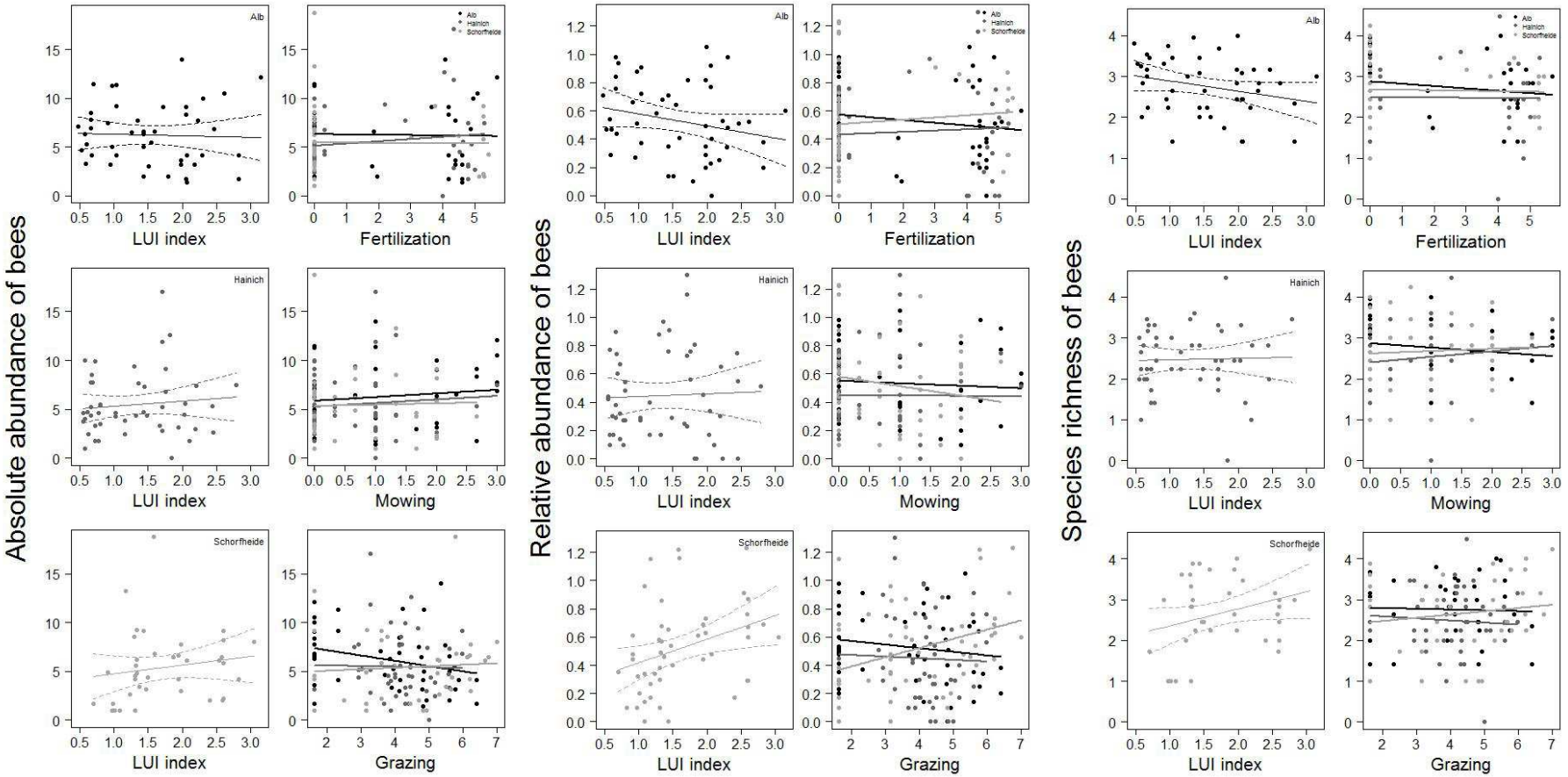

Figure 11: Relationship between bee response and land-use intensity (left panels) as well as its individual components (right panels).

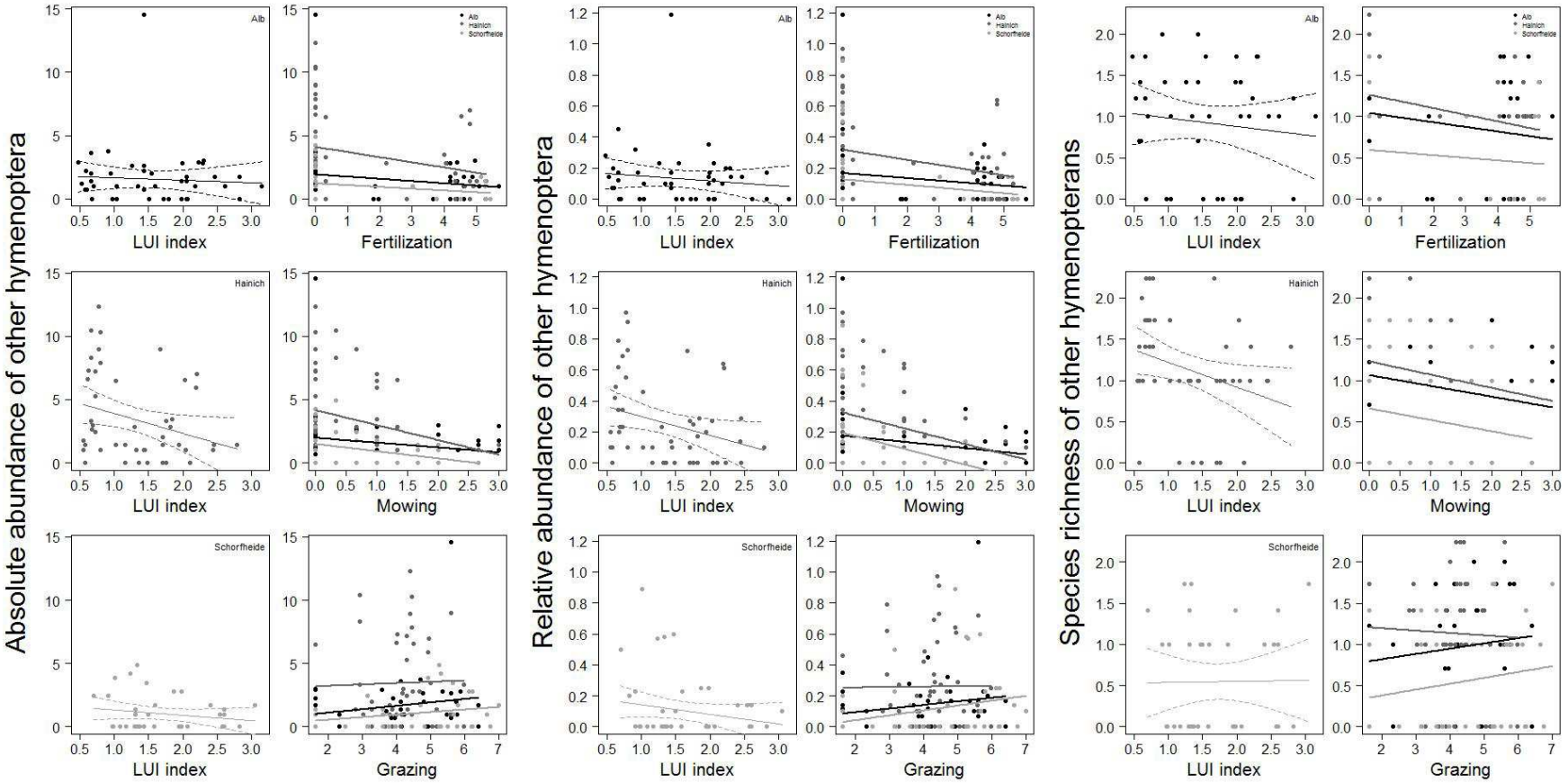

Figure 12: Relationship between response of hymenopterans (excl. bees) and land-use intensity (left panels) as well as its individual components (right panels).

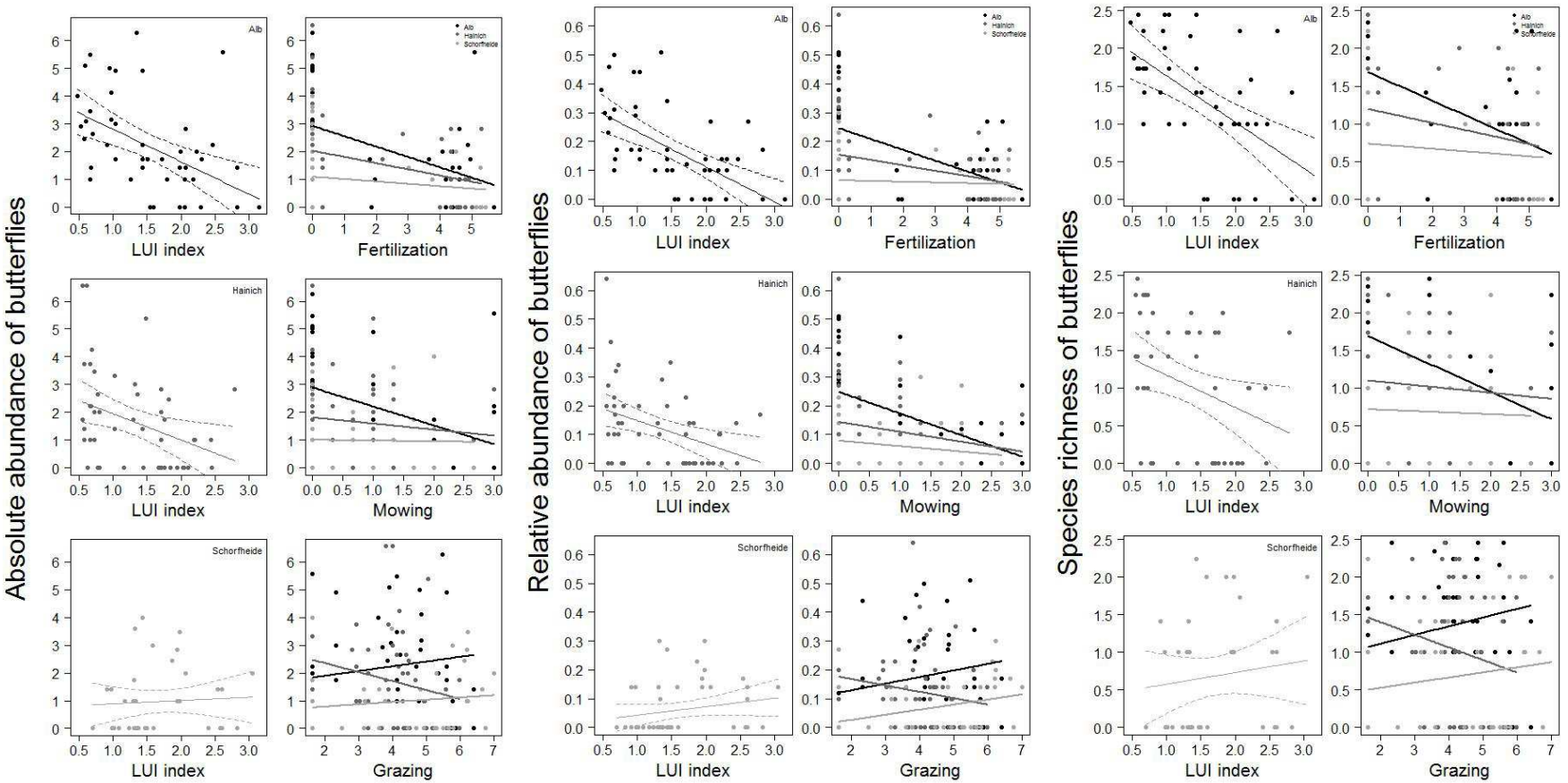

Figure 13: Relationship between butterfly response and land-use intensity (left panels) as well as its individual components (right panels).

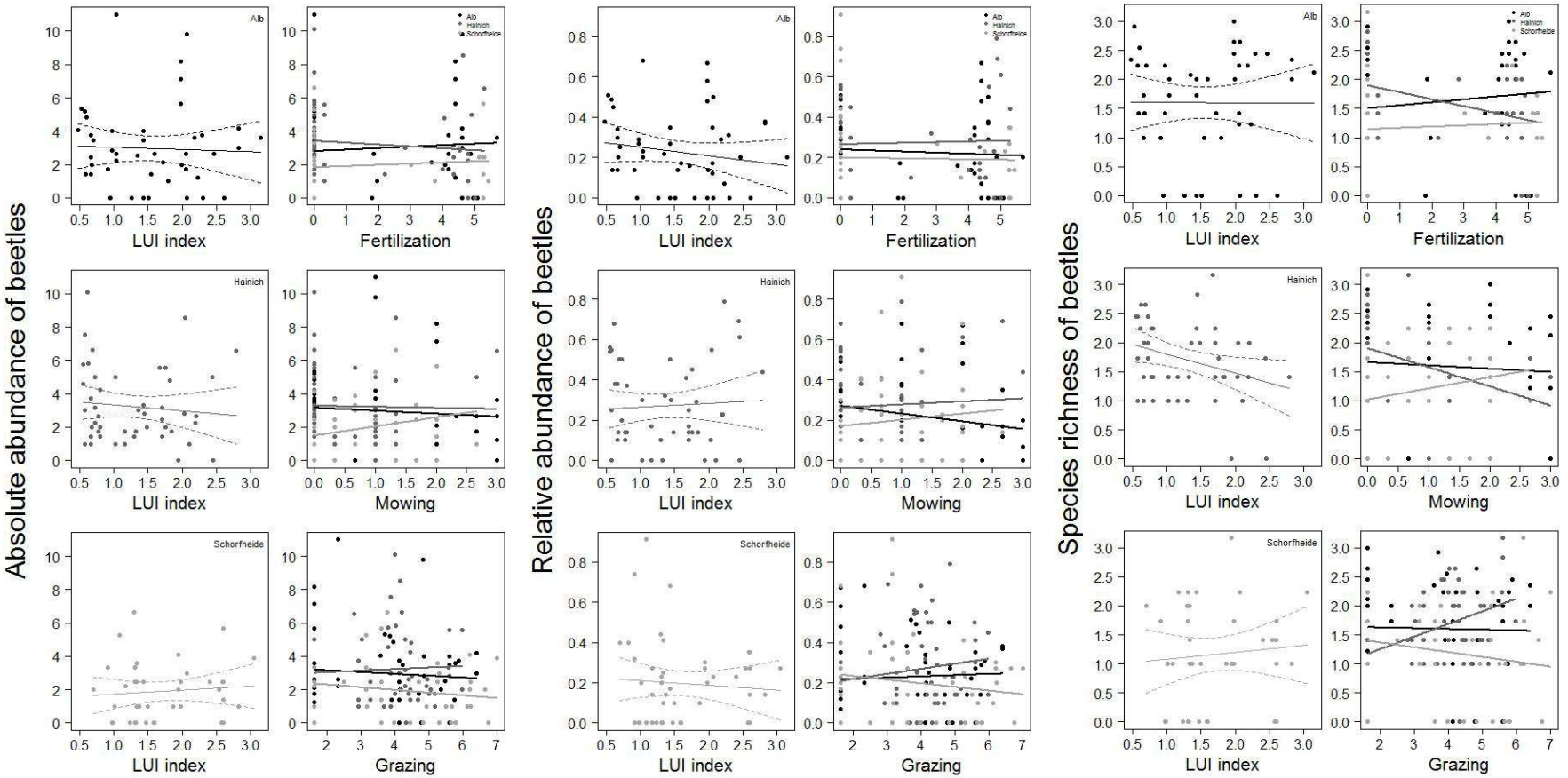

Figure 14: Relationship between beetle response and land-use intensity (left panels) as well as its individual components (right panels).

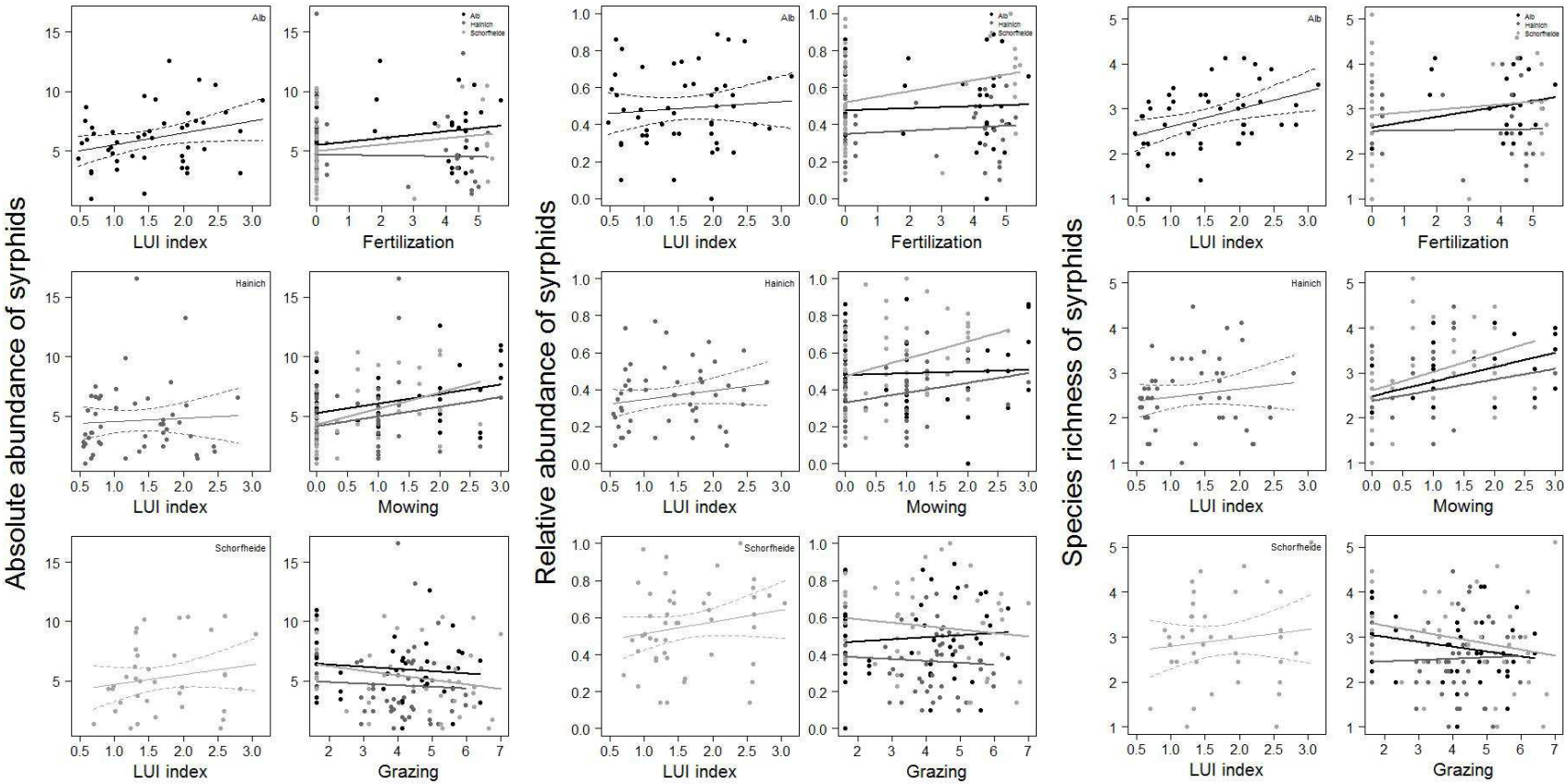

Figure 15: Relationship between syrphid response and land-use intensity (left panels) as well as its individual components (right panels).

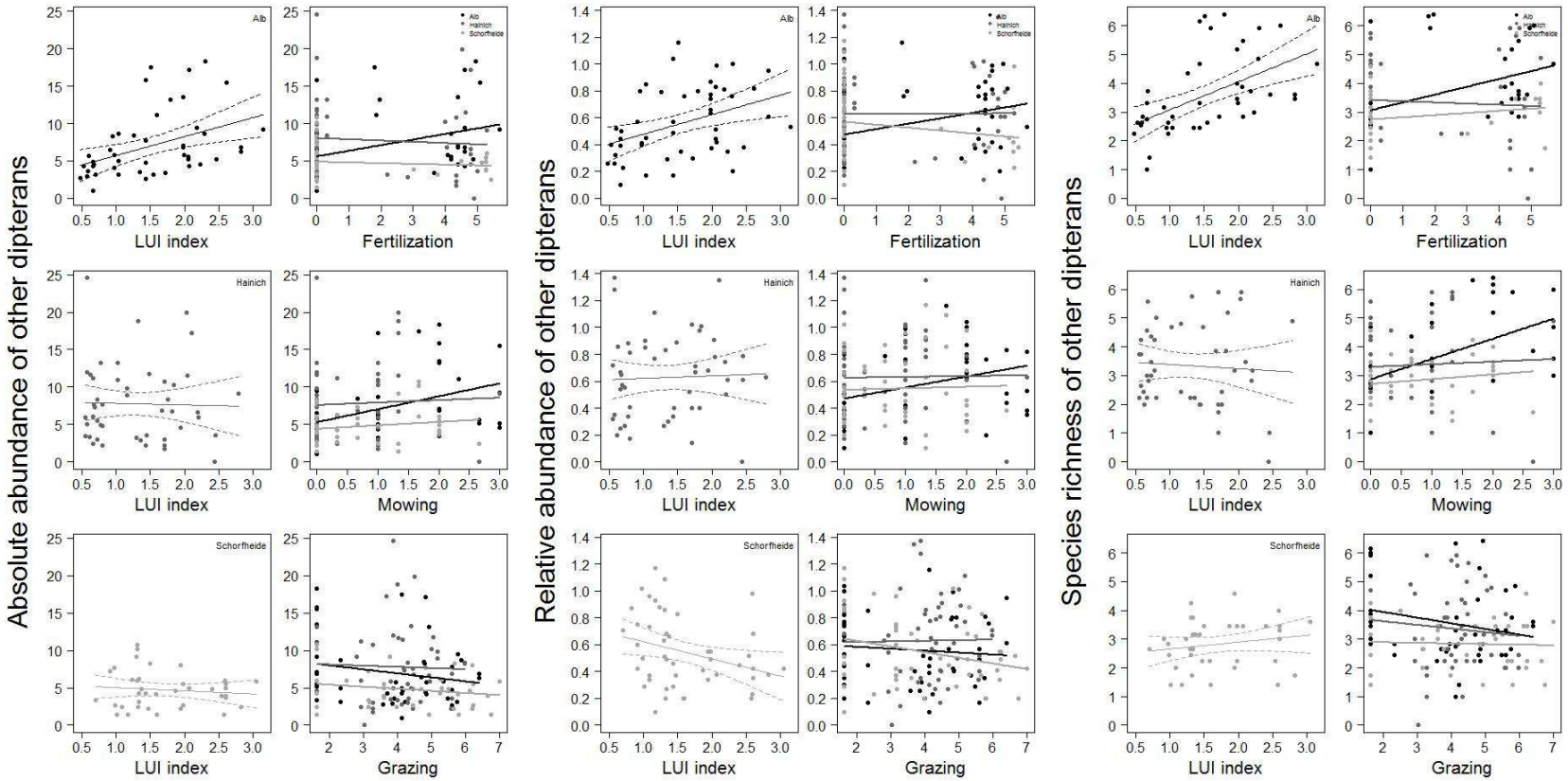

Figure 16: Relationship between dipteran response (excl. syrphids) and land-use intensity (left panels) as well as its individual components (right panels).

4.3.3 Land-use effects on plant-pollinator interactions and specialization

From a total of 25401 documented interactions 11028 were recorded in the Alb, 9649 in the Hainich and 4724 in the Schorfheide. We observed pollinator visitation in 114 out of 163 plant species in the Alb, 85/143 species in the Hainich and only 64/106 species in the Schorfheide. Moreover, plant-pollinator networks were highly structured (mean network complementary specialization ± sd: Alb: $H_2' = 0.61 \pm 0.14$, N = 49, Hai: $H_2' = 0.62 \pm 0.13$, N = 51, Sch: $H_2' = 0.65 \pm 0.23$, N = 48).

Within each Exploratory plant response to land-use intensification (r_{plants}) was independent of plant species specialization (d_j'), i.e. plants considered as highly specialized concerning their pollinator interactions did not respond more negatively to land-use intensification than more opportunistic plant species (Table 3, see Chapter 3 for results across all Exploratories). We also confirmed that the response of plant species to land-use intensification correlates to the average responses of their specific partners (E_j) not only across all Exploratories (Chapter 3) but also within each single Exploratory (Table 8).

Moreover, in all Exploratories pollinator fate ($r_{pollinators}$) was determined by the average land-use response (E_i) of the plant species they visited (Figure 17, Table 8). Additionally, in the Alb and Hainich Exploratories pollinator group identity was found to be a significant predictor for the land-use response ($r_{pollinators}$) of pollinators (Table 8). Moreover, in the Hainich Exploratory land-use intensification disproportionately affected specialized pollinators (Table 8). If pollinator specialization (d_i') was treated as a sole variable, it was a significant predictor for pollinator fate in the Alb Exploratory, too (Table 8). Species specialization d_i' differed between pollinator groups in these two Exploratories, but not in the Schorfheide (Kruskal-Wallis-Test, Alb $p < 0.0001$, Hainich $p = 0.0002$, Schorfheide $p = 0.081$; Figure A1). In the Alb and Hainich Exploratories species' specialization was highest for bees and butterflies, medium for beetles and hymenopterans (excl. bees) and lowest for syrphids and other dipterans (Figure A1, Tab A2).

Table 8: (a) Statistical model to predict species-specific plant responses to land use (r_{plants}) based on the weighted average partner response E_j (weighted $r_{pollinators}$) and specialization (d'). (b) Model to predict pollinator responses ($r_{pollinators}$) based on weighted average plant responses E_i (weighted r_{plants}) and pollinator specialization (d') and pollinator group. Complete model and main factors in univariate models are shown (ANCOVA; Type II SS).

(a)

		Complete model			Univariate model		
Exploratory	Effect	df	F	p	df	F	p
Alb	E_j	1	39.12	< **0.00001**	1	41.30	< **0.00001**
	dj'	1	0.89	0.3483	1	2.04	0.156
	$E_j \times$ dj'	1	0.24	0.6248	-	-	-
Hainich	E_j	1	9.87	**0.00237**	1	9.23	**0.00318**
	dj'	1	0.51	0.4772	1	0.14	0.705
	$E_j \times$ dj'	1	0.00	0.9846	-	-	-
Schorfheide	E_j	1	20.99	**0.00002**	1	21.43	**0.00002**
	dj'	1	0.19	0.6686	1	0.11	0.739
	$E_j \times$ dj'	1	0.50	0.4844	-	-	-

(b)

		Complete model			Univariate model		
Exploratory	Effect	df	F	p	df	F	p
Alb	E_i	1	272.84	<**0.00001**	1	369.61	<**0.000001**
	d_i'	1	0.43	0.5108	1	28.16	<**0.000001**
	pollinator group	5	3.88	**0.0019**	5	14.93	<**0.000001**
	$E_i \times d_i$'	1	5.52	**0.0192**	-	-	-
	$E_i \times$ pollinator group	5	3.02	**0.0108**	-	-	-
	d_i' × pollinator group	5	1.94	0.0866	-	-	-
Hainich	E_i	1	50.93	<**0.00001**	1	59.37	<**0.000001**
	d_i'	1	6.55	**0.0109**	1	10.88	**0.00106**
	pollinator group	5	3.60	**0.0034**	5	5.02	**0.00018**
	$E_i \times d_i$'	1	0.00	0.9727	-	-	-
	$E_i \times$ pollinator group	5	2.12	0.0630	-	-	-
	d_i' × pollinator group	5	0.71	0.6131	-	-	-
Schorfheide	E_i	1	124.50	<**0.00001**	1	133.97	<**0.000001**
	d_i'	1	0.27	0.6051	1	0.24	0.6258
	pollinator group	5	1.06	0.3808	5	1.80	0.1115
	$E_i \times d_i$'	1	0.09	0.7591	-	-	-
	$E_i \times$ pollinator group	5	1.25	0.2835	-	-	-
	d_i' × pollinator group	5	1.17	0.3260	-	-	-

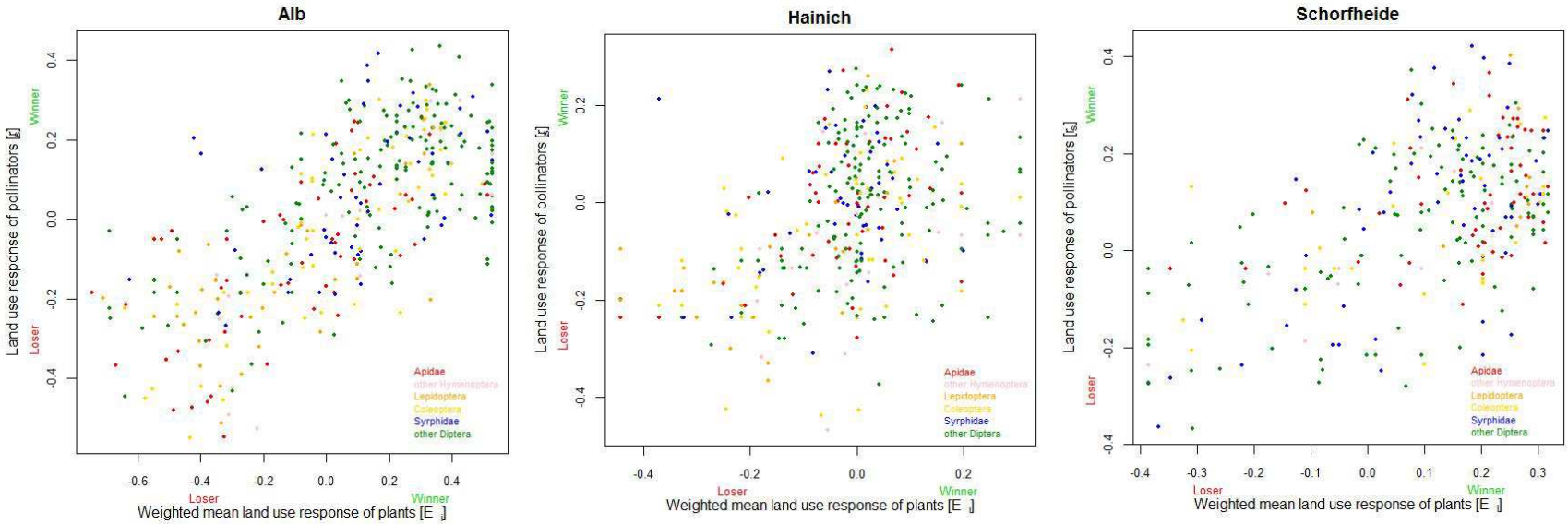

Figure 17: Interaction strength and partner identity in quantitative networks predict indirect effects of land-use intensification: Throughout all Exploratories pollinator abundance decreases in response to declines of their most frequently visited plant species.

4.4 Discussion

In grasslands, land-use management mainly consists of three different components, namely grazing, mowing and fertilization. For plant species richness it has been shown earlier that its correlations to the intensification of those components may differ in strength and even direction (Socher et al. 2012). In order to better understand the mechanisms which may entail the loss of biodiversity in managed grasslands we tried to disentangle the effects of single land-use components on species composition, abundance and diversity in plant-pollinator networks. This is a first step towards the conservation of the ecosystem service pollinators provide. Once the requirements for maintenance of high pollinator diversity and its significance for plant reproduction are understood plans for their management can be developed.

4.4.1 Land-use effects on plant communities

For plant communities it is known that increased fertilizer application and augmented mowing frequency reduce flower diversity and may deteriorate community productivity, stability and resilience (Mountford et al. 1993, Tilman and Downing 1994, Hector et al. 1999, Cardinale et al. 2007, Hector and Bagchi 2007). Fertilization in our study was negatively correlated to species richness of flowering plants in the Alb and Hainich Exploratories while fertilizer input had no significant effect on species richness in the Schorfheide. This is in line with Socher et al. (2012) who analyzed direct and indirect effects of fertilization, mowing and grazing intensity on plant species richness in the same regional context. The difference in effects between Exploratories may be related to differences in soil types, as the grasslands in the Alb and Hainich Exploratories are on mineral soils while those of the Schorfheide mainly are on wet, eutrophic organic soils (Fischer et al. 2010), e.g. conditions which make plants less dependent on additional nutrient supply. High nitrogen levels or nitrogen addition favors the biomass and seed production of grasses whereas low nitrogen levels promote herb growth, flower production and pollinator visitation (Burkle and Irwin 2010). Fertilization affects plant species richness mainly through indirect effects via increases of productivity (Crawley et al. 2005). In anthropogenic grasslands species richness declines at high levels of productivity (Adler et al. 2011) due to increased competition (Grime 1973) and

reduced light for subdominant plants (Hautier et al. 2009). These points may also explain why we found considerable lower species numbers of flowering plants both overall and per site in the Schorfheide Exploratory in comparison to Schwäbische Alb and Hainich.

Consistent with other studies our analysis showed that an increase in mowing intensity goes along with a decrease in plant species richness (Hansson and Fogelfors 2000, Zechmeister et al. 2003, Knop et al. 2006). Although graphically we observed this trend in all Exploratories, the effect was pronounced significantly in the Alb only and missed significance just by a narrow margin in the Hainich. Again our results are largely consistent with Socher et al. (2012). Due to the strong ability of grasses to regrow after disturbances such as mowing, an increase in the number of cuts goes along with an increase in the abundance of grasses (Zechmeister et al. 2003). In contrast to grazing, mowing removes biomass homogeneously and thus generally selects for species with re-growth ability, favoring shallow-rooted grasses and not deeper rooted herbs and legumes. A reason for the strong effect of mowing on the species richness of flowering plants in the Alb Exploratory may be that the diversity of flowering plants per site is comparatively high in this Exploratory so that shifts in plant species composition towards grass species induced by mowing carry more weight.

In contrast to mowing grazing was positively correlated to species richness in the Alb Exploratory. Positive effects from grazing are usually attributed to the higher sward heterogeneity of grazed grassland plots through trampling and selective grazing, which increases germination and establishment of otherwise subdominant herbs (Proulx and Mazumder 1998, Rook et al. 2004). The effect of grazing intensity on plant diversity varies between different types of livestock, e.g. sheep, horses and cattle (Rook et al. 2004). Pastures grazed by sheep had the highest cover of herbs and a higher species richness compared to grasslands grazed by cattle or horses (Socher et al. 2012, Socher et al. 2013).

As in the Alb Exploratory three quarters of the pastures and mown pastures we surveyed were grazed by sheep, this may explain the overall positive effect of grazing intensity. In the other two Exploratories pastures and mown pastures surveyed were mainly grazed by cattle. However, differences in grazing effects can also be attributed to differences in soil types that influence the degree to which grazing affects sward heterogeneity and to strongly different initial species composition between the regions.

Thus, also factors which we did not consider in our statistical analysis may play a role and our explanatory variables may be confounded with factors like soil type or initial species composition and vegetation structure.

4.4.2 Land-use effects on pollinator communities

Baseline information about plant-pollinator interactions, species richness and abundance of pollinators along gradients of land-use intensity can not only provide us with a better understanding of pollination but also for maintenance of pollinator diversity and how pollinators are affected by different land-use regimes. Here it is essential to explore the land-use responses of distinct pollinator groups in detail as taxonomic and functional groups as well as rare and abundant species may respond differently to management regimes (Biesmeijer et al. 2006, Jauker et al. 2009). For example, threatened pollinator species in our study showed significant decreases in species richness in relation to land-use intensity (LUI) and fertilization in the Alb Exploratory while abundance of threatened species was positively related to land-use intensity in the Schorfheide. As threatened species are usualy rare on the landscape scale but may be very abundant locally (Kotiaho et al. 2005), our results suggest that in the Alb suitable sites for threatened species were found rather related to low land-use intensities while in the Schorfheide threatened species reached high population densities on sites related to higher land-use intensities. As discussed below in the Schorfheide Exploratory most sites are on organic soils which proved to be associated with lower species diversities than sites on mineral soils where land-use intensity is often higher in this Exploratory.

Additionally to differences in land-use responses of rare versus abundant pollinators, differences between specialist and generalist species may exist (Tudor et al. 2004, Kleijn and Raemakers 2008) and it has to be kept in mind that an absolute increase of diversity or abundance can go along with biological homogenization, e.g. that some taxa disappear while others strongly increase (Clavel et al. 2010, Filippi-Codaccioni et al. 2010). Two pollinator assemblages with equal species numbers can be completely different in terms of species composition and abundance structure. Thus, numerous authors cautioned against the use of single indicator taxa for management and conservation strategies. Our findings support their argument: The intensification of each land-use component examined in our study showed marked influence on either species

richness or abundance or composition of pollinators though the direction in which different land-use practices were related to species responses varied between pollinator groups and regions. For example, an increase in compound land-use intensity (LUI) was positively related to overall pollinator species richness and abundance in the Alb, but a closer look revealed opposing land-use responses of different pollinators groups. Increases in overall pollinator abundance and species richness going along with increases in mowing frequency and fertilization were driven by the enhancement of abundances and richness of syrphids and other dipterans. We observed simultaneous declines in bee diversity as well as in absolute and relative abundance and species richness of butterflies (Table 7 and A1). In relation to intensification species richness of butterflies as well as absolute and relative abundance also decreased in the Hainich and dipteran diversities increased in the Schorfheide. Such taxon-specific differences match the finding of opposing responses to agricultural intensification in bees and syrphids from Jauker et al. (2009) and Biesmeijer et al. (2006) as well as the results from Börschig et al. (2013) who observed decreasing abundance and species richness of butterflies with increasing land-use intensity in the Alb and Hainich, but not in the Schorfheide Exploratory. The latter assumed that in the Schorfheide region the species pool of butterflies was too small to detect changes in diversity with increasing land-use intensity. They further suggest that the regional lack of calcareous grasslands, which are believed to be an important habitat of high butterfly and overall insect diversity (van Swaay 2002), might account for the small butterfly species pool in the Schorfheide study sites. As we detected only eleven butterfly species in the Schorfheide, but 27 species in the Hainich and even 41 species in the Alb, where calcareous grasslands were most abundant, we subscribe to their explanatory statement. Moreover, butterflies in the Schorfheide were the taxon less specialized concerning feeding niches in our study (Table A2) and therefore may be less dependent on certain food resources. Though diversity trends were inconsistent between regions, Börschig et al. (2013) showed that with increasing land-use intensity species traits in the butterfly community change from specialist to generalist characteristics in all regions. Equal results were found by Simons et al. (2015) in a multi-taxa approach that revealed consistent shifts in arthropod species traits towards more mobile and less specialized species with increasing land-use intensity.

Generally flower-visitors in intensively managed grasslands have to be able to cope with frequent habitat disturbance as well as unreliable and low diverse food resources. In terms of their traits generalist species, e.g. concerning feeding niches or larval habitats are believed to be less prone to disturbance than specialist species (McKinney 1997). The consistently low species specialization in syrphids and other dipteran species (Table A2) indicates that they do not depend as heavily on preferred plant species as bees and butterflies do and is in line with former studies that observed low mean species specialization in dipterans as well as an increase of plant-fly interactions with increasing land-use intensity (Weiner et al. 2011).

Concerning individual land-use components fertilization intensity may influence pollinators rather indirectly via changes in plant diversity and composition. In the Alb Exploratory we observed parallel declines plant species richness and species richness of butterflies as well as a decline in bee diversity. For bees and butterflies it is known that their species richness is positively correlated to plant diversity, although it is not sure if there is a causal link or if plants and their visitors respond similarly to other environmental factors (Steffan-Dewenter and Tscharntke 2001, Hawkins and Porter 2003). However, pollinator species responses to land-use proved to be highly correlated to the weighted mean species responses of their host plants and this effect was even stronger for specialized species (Weiner et al. 2014). Thus, probably resource-mediated effects are responsible for the declines of species richness in flower visiting beetles observed in the Hainich Exploratory as well. Beetles proved to be highly specialized in flower visitation there.

As in real world landscapes high fertilization intensity is correlated to high mowing frequency, which also proved to be true for our study sites, pure effects of fertilization may not always be easily disentangled from mowing effects. Thus, a mélange of true fertilization effects and effects from mowing (see below) may be responsible for the effects of fertilization intensity on some pollinator groups. For example in syrphids and other dipterans correlations to mowing intensity were much stronger pronounced than correlations to fertilization. Nonetheless, fertilization intensity may have positive effects on species richness and abundance of dipteran species as it enhances productivity and thus plant biomass and vegetation height. Vegetation height had a positive effect on richness and abundance of syrphids in other studies (Sjödin et al. 2008).

In relation to mowing temporal declines in diversity and abundance of pollinators were observed and the timing and frequency of mowing had marked effects on insect species composition in grasslands (Bulan and Barrett 1971, Morris 1981, Kruess and Tscharntke 2002, Knop et al. 2006). Mowing may affect pollinators either directly by disruption of life cycles (Johst et al. 2006) or indirectly by a frequent unselective removal of food resources and by favoring plant species with a high re-growth ability after disturbance thus changing plant species composition (Fenner and Palmer 1998, Knop et al. 2006). Additionally, mowing as well as high grazing intensity may destroy larval habitats and are detrimental to immobile larvae. Yet, contrarily to grazing which creates a spatially heterogeneous sward structure by different livestock activities like trampling and dung deposition, high mowing intensity creates a rather homogeneous sward structure dominated by few species and a high proportion of grasses. The observed negative effects of high mowing intensity on butterflies, beetles, bees and other hymenopterans may be subscribed to such indirect effects via declines in the number of flowering plant species and compositional changes in plant composition as well as to direct effects concerning life-cycle disruption. The identified positive relation between mowing intensity and syrphids as well as other dipterans on the other hand may be attributed to the observation that intensively used meadows offer a higher abundance of easily exploitable flowers from the genus Asteraceae and Apidaceae which are readily visited by dipterans (Weiner et al. 2011). Adult syrphids are mainly pollen eaters and feed preferably on shallow flowers offering a lot of pollen (Kevan and Baker 1983). As such flowers usually possess exposed nectar sources they can be exploited by a wide range of rather short-tonged other dipterans as well.

Similarly to mowing high grazing intensity leads to temporally removal of flowers which may go along with intermittent declines in pollinator diversity. However, grazing may also have positive effects on pollinator diversity as it promotes and sustains high sward heterogeneity, produces nesting sites of bare soil for ground-nesting wild bees and other insects with endogeic larvae, fosters important pollen and nectar resources for a high variety of pollinators and prevents the succession of mono-dominant grass species (Beil and Kratochwil 2004). Additionally, pastures feature a high vegetation complexity and sward heterogeneity offering a variety of microclimates (Morris 2000). These characteristics may account for the positive relation of grazing intensity we

observed in bees and beetles. Additionally to the high diversity of flowering plants in pastures, increases of bee diversity and relative abundance may be explained by breeding strategy. Bees, collect pollen and nectar for their offspring and repeatedly need to return to the brood cells after foraging (Kleijn and van Langevelde 2006). Bee diversity and abundance, especially in small and less mobile species (Gathmann and Tscharntke 2002), may be higher in grasslands offering nesting sites. However, also general landscape context and other factors which we could not consider as explanatory variables in our models may play a role for species composition, abundance and diversity of pollinators in relation to land-use intensification.

4.4.3 Land-use effects on plant-pollinator interactions and specialization

Across all Exploratories our plant-pollinator interaction networks proved to be highly structured. The mean network specialization level (H_2') found in each Exploratory corresponds very well to other plant-pollinator networks examined (Blüthgen et al. 2007, Fründ et al. 2010, Weiner et al. 2011). Corresponding to results from earlier studies (Weiner et al. 2011) in the Alb and Hainich Exploratory mean species specialization per pollinator group (d_i') was highest for bees. Moreover, in the Alb species specialization of butterflies and beetles was significantly higher than specialization of other hymenopterans and dipteran species which was echoed in trend in the Hainich, too. Contrarily, in the Schorfheide pollinator groups did not differ in mean species specialization per group. This result may explain why pollinator group identity as well as species specialization played a role for pollinator response to land-use intensification in the Alb and Hainich, but not in the Schorfheide Exploratory (see below).

Although land-use responses of plants and pollinators strongly varied between regions as well as between taxonomic pollinator groups, we found that within each Exploratory responses of plants and pollinators were determined by species specialization and the average land-use response of their interaction partners. The response of plant species to land-use intensification corresponded to the average responses of their specific pollinators. In return, pollinators responded negatively to land use if the plant species they frequently visit declined in response to management intensification, so that a linkage between a pollinator's response to land-use and the response of the plant species

it visits can be assumed. This results confirm the findings across Exploratories from Weiner et al. (2014). Also Schaffers et al. (2008) demonstrated that local plant species composition was the most effective predictor of arthropod assemblage composition. Yet, while in the plants we investigated the land-use response of a plant species was not affected by its specialization, specialized pollinators were disproportionally affected by land-use intensification in the Hainich and in the Alb Exploratory where pollinator groups differed in mean species specialization. Scheper et al. (2014) as well as Kleijn and Raemakers (2008) identified the decline of preferred host plant species as a main factor associated with the decline of wild bee species and bumblebees and therefore stressed the importance of maintaining the preferred host plant species in order to conserve bee diversity. Accordingly, our results suggest that pollinator species are especially at risk if specialized on few resources. Our findings further indicate that some plant species may only prosper under specific management regimes and that pollinators associated with this plant species are therefore restricted to the same habitat, especially if specialized on certain resources. In turn, a negative direct response of effective pollinators to land use, e.g. via disruption of live-cycles may cause declines in the plant species they effectively pollinate in the long term.

We conclude that while species that in their interactions are highly redundant to other species may not affect the community diversity, stability and resilience such species in contrast may be unable to compensate the loss of species that show high complementarity in resource use i.e. functional niche specialization. Thus, stability and resilience within pollination networks characterized by high complementarity (Blüthgen et al. 2007) may be at risk. Moreover, compositional changes in the pollinator community from taxa and species rather specialized like many bees and butterflies to taxa and species more generalized, e.g. syrphids may have considerable economic influences in landscapes with high land-use intensity. For crops like oilseed rape pollination efficiency of wild bees is be five-fold higher than for syrphids (Jauker et al. 2012). However, management recommendations aiming on the conservation of plant and pollinator species cannot easily be adopted between regions as the regional context has strong impact on the strength and direction of how plants and pollinators respond to single land-use components.

Appendix

Table A1: Response of plant and pollinator diversities to land-use intensity (LUI) and its individual components.

Response variable	Region		LUI index			Fertilization intensity			Mowing intensity			Grazing intensity		
		N	R^2	RMSE	*p*	R^2	RMSE	*p*	R^2	RMSE	*p*	R^2	RMSE	*p*
Plant diversity	Alb	49	0.08	0.56	0.05137	0.12	0.55	**0.01279**	0.11	0.55	**0.01793**	0.07	0.56	0.06031
	Hainich	51	0.10	0.53	**0.02747**	0.07	0.53	0.06138	0.05	0.54	0.11871	0.01	0.55	0.59310
	Schorfheide	48	0.01	0.47	0.49922	0.00	0.47	0.75777	0.00	0.47	0.94291	0.01	0.47	0.56224
Pollinator diversity	Alb	49	0.01	0.82	0.42512	0.01	0.82	0.61459	0.03	0.82	0.25889	0.00	0.83	0.63160
	Hainich	51	0.01	1.19	0.52221	0.01	1.19	0.50748	0.00	1.19	0.96638	0.01	1.19	0.53859
	Schorfheide	48	0.17	1.10	**0.00315**	0.06	1.17	0.09549	0.00	1.21	0.99351	0.08	1.15	**0.04509**
Bee diversity	Alb	49	0.12	0.49	**0.01396**	0.10	0.50	**0.02698**	0.12	0.49	**0.01433**	0.03	0.52	0.22945
	Hainich	51	0.01	0.55	0.43432	0.00	0.55	0.71502	0.04	0.54	0.18444	0.00	0.55	0.86230
	Schorfheide	48	0.15	0.62	**0.00688**	0.02	0.67	0.40979	0.00	0.68	0.87613	0.09	0.65	**0.04796**
Diversity of other hymenopterans	Alb	49	0.01	0.60	0.55583	0.02	0.59	0.35557	0.02	0.59	0.28245	0.01	0.60	0.55682
	Hainich	51	0.10	0.51	**0.02778**	0.07	0.52	0.07666	0.03	0.53	0.20874	0.01	0.54	0.56444
	Schorfheide	48	0.01	0.59	0.55348	0.00	0.59	0.66878	0.04	0.58	0.16609	0.06	0.57	0.10036
Butterfly diversity	Alb	49	0.27	0.58	**0.00013**	0.27	0.58	**0.00012**	0.25	0.59	**0.00024**	0.10	0.64	**0.03013**
	Hainich	51	0.08	0.72	0.06206	0.03	0.73	0.20863	0.00	0.75	0.80266	0.03	0.73	0.20862
	Schorfheide	48	0.05	0.67	0.12823	0.00	0.69	0.83572	0.01	0.69	0.54337	0.08	0.66	0.05399
Beetle diversity	Alb	49	0.01	0.77	0.52376	0.00	0.77	0.77110	0.03	0.76	0.25527	0.02	0.77	0.36429
	Hainich	51	0.11	0.52	**0.02033**	0.19	0.50	**0.00251**	0.19	0.50	**0.00192**	0.15	0.51	**0.00755**
	Schorfheide	48	0.02	0.78	0.35013	0.00	0.79	0.69176	0.00	0.79	0.69967	0.00	0.79	0.96681
Syrphid diversity	Alb	49	0.08	0.55	**0.04822**	0.04	0.56	0.14804	0.08	0.55	0.05569	0.00	0.57	0.69231
	Hainich	51	0.04	0.56	0.20787	0.01	0.57	0.58843	0.02	0.56	0.29199	0.03	0.56	0.28423
	Schorfheide	48	0.06	0.63	0.09098	0.03	0.64	0.22311	0.05	0.64	0.14262	0.00	0.66	0.97670
Diversity of other dipterans	Alb	49	0.14	0.89	**0.00712**	0.07	0.93	0.06228	0.21	0.86	**0.00105**	0.01	0.96	0.50828
	Hainich	51	0.03	0.97	0.27631	0.01	0.98	0.62383	0.00	0.98	0.82837	0.03	0.97	0.26428
	Schorfheide	48	0.10	0.69	**0.03305**	0.08	0.69	**0.04961**	0.00	0.73	0.88676	0.04	0.71	0.16892

Model fit is expressed as Pearson correlation coefficient (R^2) and root mean square error (RMSE), in addition to significance level (*p*). Significant fit ($p < 0.05$) was marked boldface. Additionally, positive correlations are highlighted in light grey, negative ones in dark grey. Number of sites (N) is shown for each response.

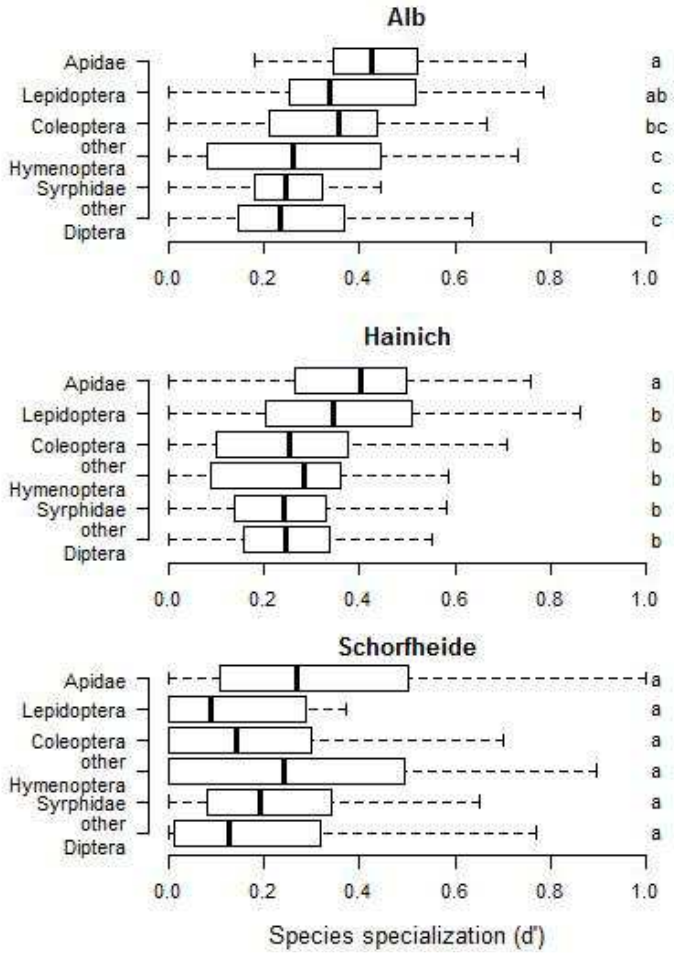

Figure A1: Comparison of weighted mean pollinator specialization (d_i`) between different pollinator groups per Exploratory. Different letters indicate significant differences according to Nemenyi Damico Wolfe Dunn post-hoc test.

Table A2: Mean specialization and land-use response per pollinator group and Exploratory

Pollinator group	N	mean d'	mean rho
Alb			
Apidae	69	0.43 ± 0.16	-0.08 ± 0.20
Hymenoptera	26	0.29 ± 0.25	-0.01 ± 0.24
Lepidoptera	41	0.38 ± 0.23	-0.12 ± 0.19
Coleoptera	59	0.33 ± 0.19	0.09 ± 0.22
Syrphidae	63	0.26 ± 0.14	0.07 ± 0.16
Diptera	205	0.27 ± 0.18	0.00 ± 0.16
Hainich			
Apidae	62	0.40 ± 0.20	0.01 ± 0.14
Hymenoptera	25	0.26 ± 0.19	-0.05 ± 0.17
Lepidoptera	27	0.36 ± 0.23	-0.12 ± 0.14
Coleoptera	57	0.25 ± 0.19	-0.01 ± 0.15
Syrphidae	54	0.25 ± 0.17	0.02 ± 0.13
Diptera	178	0.28 ± 0.19	-0.06 ± 0.14
Schorfheide			
Apidae	70	0.33 ± 0.29	0.10 ± 0.13
Hymenoptera	15	0.27 ± 0.27	0.04 ± 0.17
Lepidoptera	11	0.17 ± 0.21	0.11 ± 0.13
Coleoptera	39	0.20 ± 0.23	0.04 ± 0.15
Syrphidae	64	0.22 ± 0.18	0.08 ± 0.19
Diptera	133	0.19 ± 0.20	0.06 ± 0.15

5. Pollen amino acids and flower specialization in solitary bees

This chapter has been published as:
Weiner, C.N., Hilpert, A., Werner, M., Linsenmair, K.-E., Blüthgen, N. (2010): ***Pollen amino acids and flower specialization in solitary bees.*** *Apidologie.*

Summary

Pollen nutrient composition could be important in host plant selection of oligolectic bees. In this study, pollen samples from 142 plant species were analysed separately for water soluble and protein-bound amino acids. The composition of amino acids varied strongly between plant species, but taxonomically related species had a similar composition. All plant species contained the entire set of essential amino acids, although some in small quantities. Total concentration of free and protein-bound amino acids was significantly lower in pollen sources used by oligoleges than in other pollen sources. Pollen sources of oligoleges furthermore showed a lower concentration of essential amino acids, and deviated more strongly from the ideal composition of essential amino acids as determined for honey bees than plants not hosting oligoleges. However, this trend was not confirmed on a cruder phylogenetic plant family level, where pollen chosen by oligolectic bees was similar to other pollen.

5.1 Introduction

Most bees feed exclusively on plant pollen and nectar, representing their primary source of protein and other nutrients especially during the larval stage (Westrich 1990). While oligolectic bees depend on pollen from a single plant species, genus or family, polylectic bees use a broad spectrum of flowering plants (Cane and Sipes 2006). Traditionally, it has been assumed that polylecty was the ancestral state in bees (Michener 1954). Indeed this proved to be true for the *Hemihalictus* series in the genus *Lasioglossum* (Danforth et al. 2003), but recently growing evidence suggest that in the majority of bee lineages generalist species have evolved from oligolectic ancestors (Larkin et al. 2008, Michez et al. 2008).

The advantages of oligolecty remain largely unknown, though several hypotheses have been discussed, above all a higher proficiency of specialised bees when visiting their specific host flowers through evolutionary adaptation (Strickler 1979, Müller 2006). On the other hand, host-plant specialisation among bees could have been favoured if it

reduced interspecific competition (Thorp 1969). As all plant species visited by oligoleges are visited by polyleges as well, at least a complete escape from competition seems to be unlikely (Minckley and Roulston 2006). However, some quantitative extent of competition-avoidance could be achieved by specialising on pollen containing toxic compounds or being less nutritious and therefore visited less frequently or by fewer species. On the other hand, it has been suggested that oligolectic bees specialise on plant pollen with higher nitrogen content but this hypothesis is lacking in phylogenetically sound evidence so far (Budde et al. 2004). Pollen nutritional value has been mostly judged by its crude protein content (Day et al. 1990), estimated based on pollen nitrogen concentration multiplied by 6.25 (e.g. Rabie et al. 1983). This conversion factor may not be appropriate for pollen (Roulston and Cane 2000). Moreover, protein content may not adequately reflect the availability and composition of amino acids. Two diets containing the same protein content may differ in nutritional value due to a lack or imbalance of essential amino acids (Standifer 1967).

Insects and other animal taxa have relatively similar basic nutritional requirements, including the spectrum of essential amino acids (De Groot 1952). It has been demonstrated that dietary protein content is crucial for reproduction, growth and longevity of bees and other insects (Gilbert 1972, Roulston and Cane 2002). Preferences for diets with higher amino acid content have been documented in studies on butterflies (Erhardt and Rusterholz 1998), ants (Blüthgen and Fiedler 2004), parasitoid wasps (Wäckers 1999) and honey bees (Alm et al. 1990). The ideal composition of essential pollen amino acids (arginine 11%, histidine 5%, isoleucine 14%, leucine 16 %, lysine 11%, methionine 5%, phenylalanine 9%, threonine 11%, tryptophan 4%, valine 14%) determined for the honey bee, *Apis mellifera*, by De Groot (1953) were very similar to those of other animals (Nation 2002). Thus, it can be assumed that bees do not vary significantly in their nutritional requirements concerning relative amino acid composition.

We focussed on qualitative as well as quantitative pollen amino acid composition and balance of amino acids. Our goal was to find out whether the pollen of plants selected by oligolectic bee species differs in its chemical composition compared to the pollen of plants not hosting oligoleges. We tested whether pollen sources of oligoleges contained either a significantly higher or lower (1) total amino acid content or (2) balanced

composition of essential amino acids, (3) and deviation from an ideal composition of essential amino acids proposed by De Groot (1953) than plants not hosting oligoleges.

5.2 Methods

5.2.1 Pollen collection and analysis

Pollen from 142 plant species was sampled and analysed for its amino acid composition (Table 9). The nomenclature followed Wisskirchen and Haeupler (1998). Among these plants only five species may not be regularly visited by bees (namely *Caltha palustris* L., *Circaea lutetiana* L., *Erophila verna* L., *Sambucus nigra* L., *Silene latifolia* Poir.). However, excluding the plants from the analysis did not affect the overall results. Ninety-one of the sampled species have been either confirmed to be visited by oligoleges through pollen analysis from bee pollen scopa and/or observations (Westrich 1990, Müller et al. 1997, Müller 2006) or belong to plant genera known to host oligolectic bees. We included all species belonging to a plant genus visited by oligoleges into this group, as most oligoleges are assumed to be specialised on the genus or family level (Minckley and Roulston 2006), and observations may not cover all potential pollen host species. This yielded a total of 91 plant species hosting oligoleges and 51 plant species not hosting oligoleges. Twenty-nine plant species hosting oligoleges belonged to the family of Asteraceae, 11 species to the family of Lamiaceae. Such families with high replication may be assumed to be overrepresented in the results on the species level. We therefore present an additional test where amino acid values have been pooled for each of the 41 plant families to check whether patterns were consistent on this crude phylogenetic level ($N_{oligolectic}$ = 22 and $N_{generalised}$ = 26 families, Table 9). In families containing plants visited and plants not visited by oligoleges, we pooled plants for each category separately, which resulted in seven plant families occurring twice.

So far, most studies analysed bee-collected rather than hand-collected pollen and were based on a few plant taxa only (references in: Roulston and Cane, 2000, but see Wille et al. 1985). The analysis of bee-collected pollen is problematic as bees add substantial amounts of nectar to pollen loads (Müller et al. 2006, Leonhardt et al. 2007). This creates an unknown bias caused by nectar derived sugars accounting for up to 40 % of the pollen pellet's dry weight (Roulston and Cane 2000). Any analysis of pollen pellets

that disregards the added weight of nectar sugars to the pellets greatly underestimates the concentration of proteins in the pollen itself. This bias can not be removed by a standardized multiplier (Roulston and Buchmann 2000).

We therefore attempted to discover differences in the pollen nutritive value using hand-collected pollen samples only. For each sample, depending on pollen amount per plant species, pollen from 2-400 flower heads was pooled to yield sufficient amounts for analysis (0.08 - 9.6 mg). Large samples were subsampled for multiple determinations. As manual grinding of pollen using a mortar and a pestle prior to extraction did not change results in terms of total amino acid content (Wilcoxon; $Z = 1.54$, $p = 0.12$, $N = 8$ plant species) samples were not ground. The overall trend even showed higher contents in untreated pollen (on average 6.15 µg/mg). Each sample was checked for contaminations under a stereo microscope and then frozen at -20 °C until it was prepared for analysis by drying over night at 30 °C. Longer drying did not further decrease pollen dry weight.

Free and protein-bound amino acids were measured separately with an ion exchange chromatograph (Biotronik, amino acid analyser LC 3000). For analysis of water soluble amino acids, usually 3-5 mg (dry weight) pollen was extracted with 100 µl water for 30 min in an ultrasonic bath (EMAG, Emmi 20HC) and afterwards for 60 min in the refrigerator. After centrifugation (15 000 g) and membrane filtration for 10 min, the sediment was saved for later analysis of the amino acids of the protein fraction. The supernatant was poured into a new microcentrifuge tube, boiled for 2 min at 100 °C, and cooled in ice to room temperature before a second centrifugation for 5 min. Afterwards 50 µl of the supernatant was extracted with 10 µl 12.5% 5-Sulfosalicylic acid in the refrigerator for 30 min for precipitation of proteins. Ten minutes of centrifugation followed and 50 µl of the supernatant plus 50 µl thinning buffer were poured into a fresh tube, mixed, and pipetted in a membrane filter (Vecta Spin) before a last centrifugation for 5 min and adjacent measurement in the amino acid analyser.

For analysis of the amino acids of the protein fraction 200 µl 6 N HCl_3 were added to the sediment, the sample was mixed, boiled for four hours at 100 °C, and cooled to room temperature. 10 min of centrifugation followed. The supernatant was poured into a new tube and evaporated at 100 °C. Afterwards the sample was re-dissolved in 200 µl of water, immediately cooled to room temperature, and centrifuged again (10 min).

Subsequently 100 µl of the supernatant were mixed with 20 µl 12.5% sulphosalicylic acid and extracted 30 minutes in the refrigerator before short mixing and centrifugation for another 10 minutes followed. 100 µl of the supernatant and 100 µl sample rarefaction buffer was transferred into a new microcentrifuge tube. Then all was pipetted through a membrane filter, centrifuged for 5 minutes and transferred into a new microcentrifuge tube for further rarefaction with sample rarefaction buffer (1:5) before measurement.

The experimental variability of our technique yields a median coefficient of variation (CV = standard deviation / mean) of 0.383, with a median standard deviation (SD) of 8.52 µg/mg pollen (n = 91 repeatedly measured pollen samples). It is much smaller than the variability between samples of the same species varying in date or place of collection (median CV = 1.084, median SD = 12.16 µg/mg; n = 31 pollen samples of the same species). If pollen from a plant species was analysed in more than one sample, for consistency we included only the sample with the highest pollen dry weight into statistical analyses. However, there was no trend towards higher amino acid concentration in samples higher in weight (paired t-Test, $t = 0.66$, $p = 0.707$, $n = 91$ pairs). We compared total amino acid content yielded with our method to protein content of the same samples analysed in Bradford assays. Our results are linear correlated ($y = 0.76x + 44.61$, $R^2 = 0.91$) and slightly higher for each of the plant species analysed. Besides, our results are comparable to those of Standifer (1967).

5.2.2 Statistical analysis

The composition of pollen amino acids was examined using non-metric multidimensional scaling (NMDS), employing a Bray-Curtis similarity matrix, two dimensions, and 1000 runs. Statistics were conducted in R 2.6 (R Development Core Team 2006) using the "metaMDS" command and 1000 iterations (R-package vegan 1.8.2). Amino acid composition data were entered as molar proportions (amino $acid_i$ [µMol g^{-1}] / total amino acid concentration [µMol g^{-1}]) based on dry weight. To analyse differences among plant families and between the groups of plants hosting vs. not hosting oligoleges analyses of variance using distance matrices ("adonis" command, R-package vegan) were conducted. The balance of the proportions of amino acids was measured as standardized evenness derived from Simpson's diversity index:

$$E_p = \frac{\left(1/\sum_{i=1}^{I} p_i^{\,2}\right)-1}{I-1},$$

where p_i is the molar proportion of each amino acid i of the total concentration of I amino acids. E_P approaches 0 for the most imbalanced composition and 1 for a perfectly homogenous composition with each amino acid occurring in the same proportion. The deviation of essential pollen amino acid composition from the ideal composition determined for the honey bee by De Groot (1953) were measured as Bray-Curtis distances. Mann-Whitney U-tests (two-tailed) were conducted to examine whether plants hosting oligolectic bees differed in any parameter from plants not known to host oligoleges. All analyses were performed for total amino acids (free plus protein-bound) and separately for the free amino acids alone. Moreover, separate analyses were performed for the whole spectrum of amino acids (see Figure 18) and only for the essential ten, namely arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine (De Groot 1952).

5.3 Results

Plants differed strongly in their composition of pollen amino acids especially in the proportions of free and protein-bound amino acids (Figure 18). Closely related plant species plotted together on the ordination diagram, showing similar pollen chemistry (Figure 19). Differences across families were significant (ADONIS; $R^2 = 0.677$, $p < 0.01$). However, plant species supporting oligolectic bees did not differ significantly from other plants in overall amino acid composition of pollen ($R^2 = 0.002$, $p = 0.58$) and are scattered among them (Figure 19).

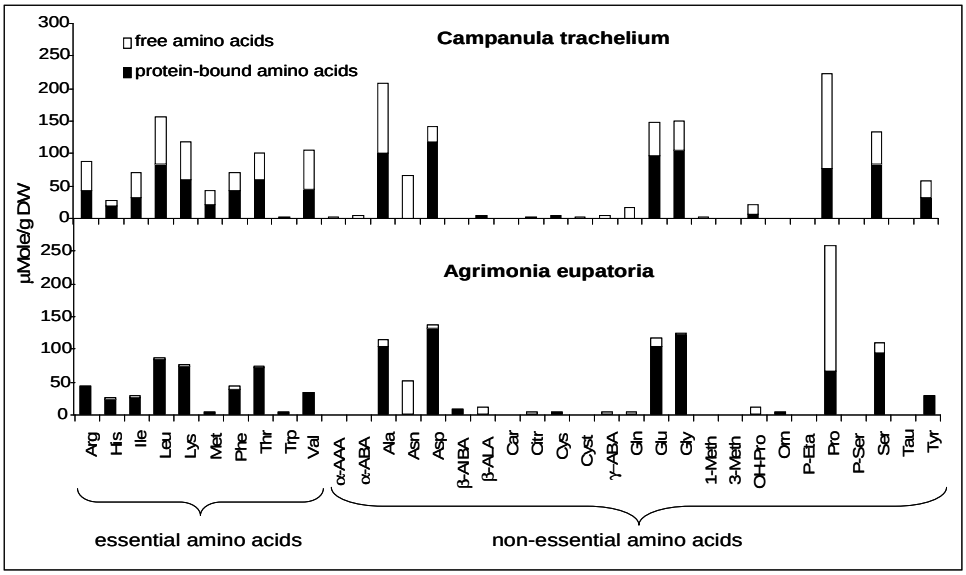

Figure 18: Amino acid profile of two exemplary plant species: *Campanula trachelium* vs. *Agrimonia eupatoria*. *C. trachelium* is known to host oligolectic bees unlike *A. eupatoria*. All measured amino acids and their derivates are displayed, separated into free and protein-bound amino acids. Note that the relative proportion of protein-bound amino acids differs between these species. (Arg = arginine, His = histidine, Ile = isoleucine, Leu = leucine, Lys = lysine, Met = methionine, Phe = phenylalanine, Thr = threonine, Trp = tryptophan, Val = valine, □-AAA = □-aminoadipic acid, □-ABA = □-aminobutyric acid, Ala = alanine, Asn = asparagine, Asp = aspartic acid, □-AIBA = □-aminoisobutyric acid , □-Ala = □-Alanine, Car = carnosine, Citr = citrulline, Cys = cysteine, Cyst = cystathionine, □-ABA = □-aminobutyric acid, Gln = glutamine, Glu = glutamic acid, Gly = Glycin , 1-Meth = 1-methylhistidine, 3-Meth = 3-methylhistidine, OH-Pro = hydroxyproline, Orn = ornithine, P-Eta = phosphoethanolamine, Pro = proline, P-Ser = phosphoserine, Ser = serine, Tau = taurine, Tyr = tyrosine)

Average amino acid concentrations differed significantly between pollen from plant species supporting oligolectic bees and pollen collected from plants not hosting oligoleges (Figure 20). Plants hosting oligoleges showed a significantly lower pollen quality, both in terms of total amino acid concentration and the fraction of all essential amino acids. This differentiation was found in the pooled total, but not in the fraction of free amino acids (Figure 20). However, some plant families, namely Asteraceae and Lamiaceae are overrepresented in the genus-level sample and thus shape the results on this specific level.

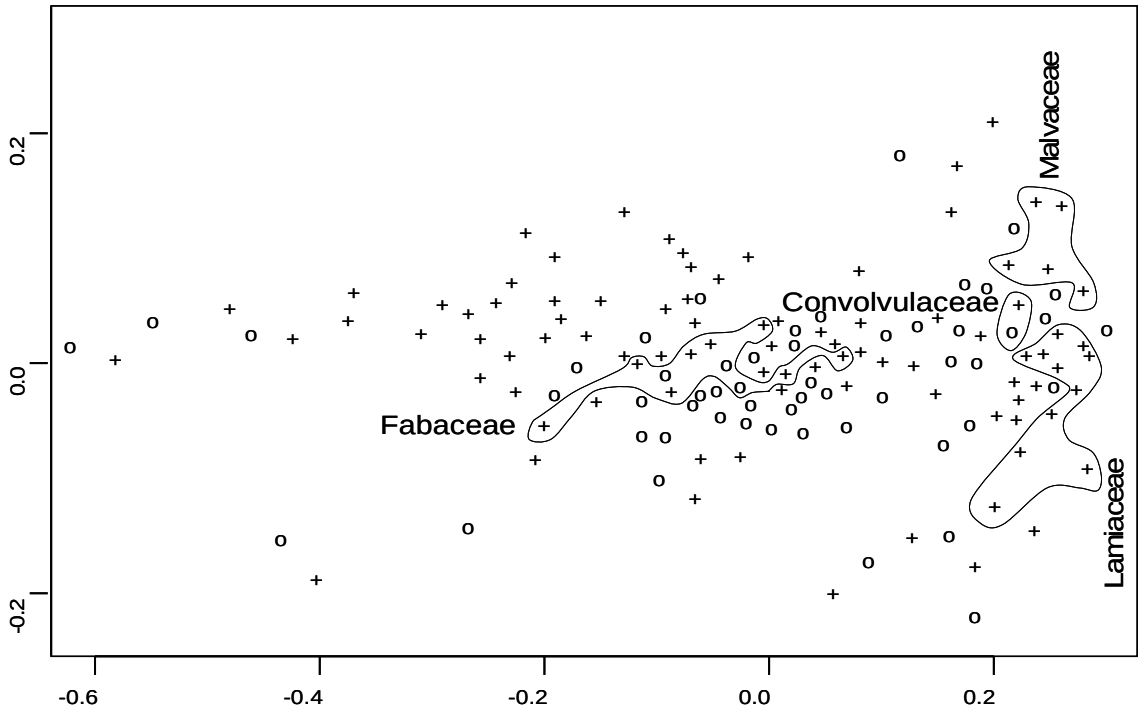

Figure 19: Taxonomic signals in pollen amino acids: closely related species often have a similar chemistry. Each symbol denotes one plant species, plants hosting oligolectic bees are displayed with "+" and plants visited solely by generalised flower-visitors with "o". Species that plot together are similar in their relative proportions of amino acids (free and protein-bound pooled). Four examples of plant families are highlighted to indicate their similar pollen composition. (NMDS, stress = 9.53, Bray-Curtis Similarity).

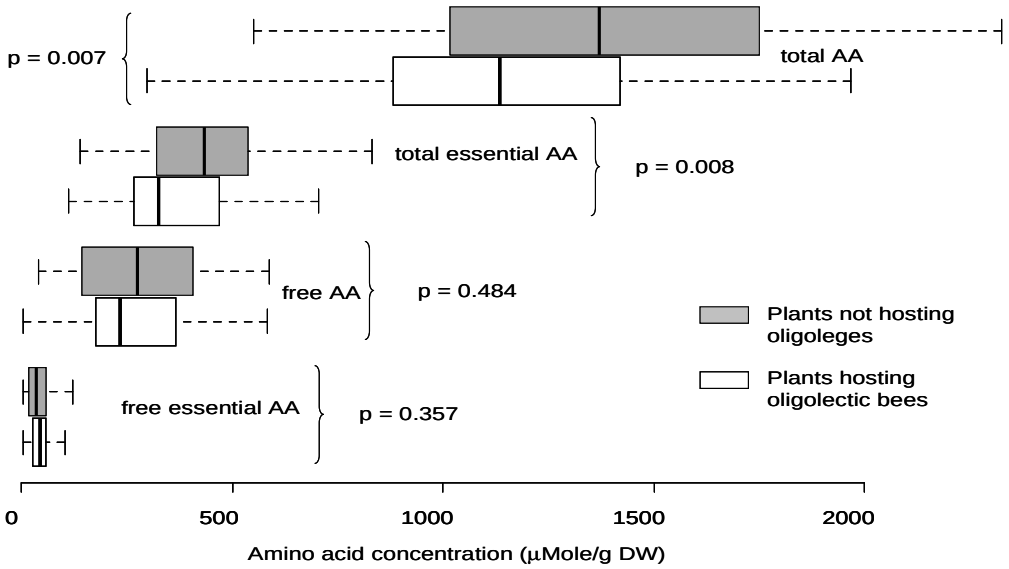

Figure 20: Amino acids (AA) compared between plants hosting oligolectic bees vs. plants not known to host oligoleges. Box whisker plots showing median, quartiles and range. Plants hosting oligoleges showed a significantly lower pollen quality in terms of total amino acid concentration (Mann-Whitney U-test; $Z = -2.69$, $p = 0.0072$) and the fraction of all essential amino acids ($Z = -2.64$, $p = 0.0082$), whereas the fractions of free and free essential amino acids did not show significant differences (all $Z \leq 0.92$, all $p \geq 0.36$) ($N_{oligolectic} = 91$, $N_{generalised} = 51$).

When data are pooled on the family level, no differences between plant families visited and families not visited by oligoleges remained (Mann-Whitney U tests for groups of compounds as in Figure 3, all $Z \leq 0.35$, $p \geq 0.64$, $N_{oligolectic} = 22$, $N_{generalised} = 26$).

The balance of amino acids (evenness) did not vary significantly between plants hosting oligolectic bees and plants not hosting oligoleges. This was true also for each of the fractions described above (all $Z \leq 0.86$, all $p \geq 0.25$, $N_{oligolectic} = 91$, $N_{generalised} = 51$ plant species). However, plant genera hosting oligoleges had a significantly less ideal composition of essential pollen amino acids on the basis determined by De Groot (1953) for honey bees than the other plants ($Z = 2.66$, $p = 0.008$). The mean (± SD) Bray-Curtis Distance between pollen and the ideal composition for pollen collected by oligolectic bees was 0.179 (± 0.03) and 0.161 (± 0.02) for pollen not known to be collected by oligolectic bees. In particular, plants hosting oligoleges contain a significantly smaller proportion of valin ($Z = 2.58$, $p = 0.0099$), isoleucin ($Z = 3.17$, $p = 0.002$), leucin ($Z = 2.08$, $p = 0.037$) and arginin ($Z = 1.98$, $p = 0.048$) but a higher proportion of histidin ($Z = 2.65$, $p = 0.008$). However, after phylogenetic correction only the result for isoleucin remains significant ($Z = 2.07$, $p = 0.039$).

Most sampled species contained the full spectrum of essential amino acids. However, tryptophan had particularly low levels (< 1.0 µMol/g) in more than one-third of the plant species analysed, and methionine was present only in traces in *Pastinaca sativa* and *Erigeron annuus*. The total concentration ranged from 0.04 µMol/g dry weight in *Silene dioica* to 15.8 µMol/g in *Corydalis cava*.

Table 9: List giving all analysed plant taxa, their assignment to one of the two tested groups (O = pollen hosts of oligolectic bees, N = not hosting oligolectic bees) and the total concentration of free and protein-bound amino acids as well as percentage of essential amino acids (AA = amino acids).

Plant name	Plant family	Oligolecty	Water-soluble AA (µg/mg)	Essential water-soluble AA (%)	Protein-bound AA (µg/mg)	Essential protein-bound AA geb (%)
Acer platanoides	Aceraceae	N	59.99	34.60	102.98	38.10
Allium cepa	Alliaceae	O	55.32	15.50	117.26	36.30
Allium ursinum	Alliaceae	O	25.19	17.60	179.88	37.40
Leucojum vernum	Amaryllidaceae	N	142.92	49.10	155.47	40.20
Daucus carota	Apiaceae	O	86.29	9.80	80.14	33.10
Pastinaca sativa	Apiaceae	O	72.48	13.40	88.33	35.60
Hedera helix	Araliaceae	O	54.49	8.80	143.65	35.60
Achillea millefolium	Asteraceae	O	24.21	26.60	56.45	33.40
Antennaria dioica	Asteraceae	O	36.80	24.90	79.64	35.90
Arctium minus	Asteraceae	O	40.33	6.70	89.51	34.50
Arctium tomentosum	Asteraceae	O	42.35	16.10	58.46	36.30
Bellis perennis	Asteraceae	O	22.53	44.90	71.52	35.80
Carduus acanthoides	Asteraceae	O	57.51	14.70	69.47	35.10
Centaurea cyanus	Asteraceae	O	47.36	30.90	91.06	37.10
Centaurea jacea	Asteraceae	O	39.37	23.30	85.85	37.00
Cichorium intybus	Asteraceae	O	34.05	24.10	87.83	34.70
Cirsium arvense	Asteraceae	O	51.28	16.10	81.67	36.40
Cirsium oleraceum	Asteraceae	O	60.94	12.00	83.51	37.80
Cirsium vulgare	Asteraceae	O	43.75	10.80	102.44	35.10
Crepis biennis	Asteraceae	O	43.92	26.40	80.26	34.50
Echinops sphaerocephalus	Asteraceae	O	47.21	10.40	91.93	34.20
Erigeron annuus	Asteraceae	O	7.44	28.20	44.09	29.90
Helianthus annuus	Asteraceae	O	21.84	52.20	92.04	35.60
Hypochaeris radicata	Asteraceae	O	50.42	21.50	96.67	35.90
Leucanthemum ircutianum	Asteraceae	O	39.82	19.80	62.24	37.30
Leucanthemum vulgare	Asteraceae	O	23.39	2.90	69.16	36.80
Matricaria recutita	Asteraceae	O	32.66	23.50	55.55	35.50
Rudbeckia fulgida	Asteraceae	O	17.37	51.10	66.62	38.60
Senecio erucifolius	Asteraceae	O	28.27	30.80	67.84	36.60
Senecio fuchsii	Asteraceae	O	33.68	24.40	75.06	35.30
Senecio jacobaea	Asteraceae	O	28.67	31.00	79.63	37.20
Tanacetum vulgare	Asteraceae	O	30.34	17.10	64.16	35.00
Taraxacum officinale section Ruderalia	Asteraceae	O	24.44	28.10	72.98	35.00
Tragopogon pratensis orientalis	Asteraceae	O	46.45	22.80	71.62	36.10
Tragopogon pratensis pratensis	Asteraceae	O	37.21	12.20	94.11	36.00
Tussilago farfara	Asteraceae	O	46.03	18.80	65.47	33.80
Impatiens glandulifera	Balsamicaceae	N	31.07	53.10	105.07	37.60
Impatiens parviflora	Balsamicaceae	N	11.11	43.10	85.74	38.60
Betula pendula	Betulaceae	N	11.87	15.40	57.48	36.50
Borago officinalis	Boraginaceae	N	52.60	3.90	167.19	38.60
Echium vulgare	Boraginaceae	O	25.11	23.90	141.28	35.90
Symphytum officinale	Boraginaceae	O	49.85	18.40	194.74	39.00
Alliaria petiolata	Brassicaceae	O	30.11	17.10	112.17	34.40
Berteroa incana	Brassicaceae	O	18.52	19.70	120.22	38.10
Brassica napus	Brassicaceae	O	24.68	21.50	142.94	38.00

Erophila verna	Brassicaceae	O	17.07	22.40	93.04	33.40
Campanula glomerata	Campanulaceae	O	34.77	18.60	156.25	38.90
Campanula patula	Campanulaceae	O	21.97	20.00	157.59	39.70
Campanula rapuncoloides	Campanulaceae	O	127.84	41.80	95.37	37.20
Campanula trachelium	Campanulaceae	O	118.99	43.80	130.42	39.30
Sambucus nigra	Caprifoliaceae	N	9.89	8.30	161.22	33.30
Viburnum lantana	Caprifoliaceae	N	20.79	4.70	131.00	30.80
Cerastium arvense	Caryophyllaceae	N	24.70	14.00	75.33	36.90
Saponaria officinalis	Caryophyllaceae	N	32.92	7.80	155.97	37.90
Silene dioica	Caryophyllaceae	N	14.61	12.00	142.36	36.70
Silene latifolia	Caryophyllaceae	N	14.72	9.00	156.14	37.70
Hypericum perforatum	Clusiaceae	N	18.01	26.20	135.14	38.60
Colchicum autumnale	Colchicaceae	N	22.44	16.60	162.83	37.90
Calystegia sepium	Convolvulaceae	N	15.08	44.20	124.51	36.50
Convolvulus arvensis	Convolvulaceae	O	9.63	37.50	114.50	37.50
Bryonia dioica	Curcubitaceae	O	27.44	16.40	157.36	37.80
Dipsacus fullonum	Dipsacaceae	O	46.16	10.50	95.66	35.70
Knautia arvensis	Dipsacaceae	O	27.25	11.90	123.56	35.60
Lathyrus pratense	Fabaceae	O	30.72	15.70	145.20	37.20
Lotus corniculatus	Fabaceae	O	45.42	7.80	174.65	36.80
Lupinus polyphyllus	Fabaceae	N	71.06	22.40	205.16	38.90
Medicago fallcata	Fabaceae	O	28.99	27.40	83.46	37.20
Medicago sativa	Fabaceae	O	23.55	6.10	141.54	36.30
Onobrychis viciifolia	Fabaceae	O	51.95	9.30	132.41	37.70
Ononis spinosa	Fabaceae	N	50.63	23.00	145.15	38.40
Securigera varia	Fabaceae	N	43.44	15.20	178.58	36.20
Trifolium medium	Fabaceae	O	57.56	16.40	166.78	38.90
Trifolium pratense	Fabaceae	O	50.54	7.00	113.65	38.90
Vicia sepium	Fabaceae	O	40.49	13.00	159.12	36.40
Corydalis cava	Fumariaceae	N	94.73	5.10	124.99	33.90
Gentiana lutea	Gentianaceae	N	12.94	60.10	117.56	39.00
Geranium pratense	Geraniaceae	N	46.53	14.00	35.44	33.30
Geranium pyrenaicum	Geraniaceae	N	56.11	6.20	54.32	36.00
Geranium sylvaticum	Geraniaceae	N	48.47	27.00	40.25	34.50
Aesculus hippocastanum	Hippocastanaceae	N	55.75	17.70	201.77	39.30
Muscari comosa	Hyacinthaceae	O	24.84	11.30	167.93	37.80
Ajuga reptans	Lamiaceae	O	30.30	18.80	186.32	39.20
Ballota nigra	Lamiaceae	O	17.38	18.40	145.31	36.80
Galeobdolon luteum	Lamiaceae	O	28.50	34.40	159.68	38.50
Glechoma hederacea	Lamiaceae	O	40.49	32.10	105.96	37.60
Lamium album	Lamiaceae	O	21.23	20.10	188.70	37.90
Lamium maculatum	Lamiaceae	O	16.63	23.80	211.07	36.60
Lamium purpureum	Lamiaceae	O	6.68	16.60	55.47	35.10
Prunella vulgaris	Lamiaceae	O	35.85	37.50	121.85	38.20
Salvia pratensis	Lamiaceae	O	31.86	34.90	105.80	40.20
Stachys recta	Lamiaceae	O	17.40	16.80	207.43	39.60
Stachys sylvatica	Lamiaceae	O	19.15	13.20	216.86	40.00
Lythrum salicaria	Lythraceae	O	19.80	11.20	89.98	37.00
Alcea rosea	Malvaceae	O	0.68	57.20	40.08	37.50
Malva alcea	Malvaceae	O	5.26	29.70	56.26	38.80
Malva moschata	Malvaceae	O	7.34	54.30	29.41	35.90
Malva neglecta	Malvaceae	O	11.62	35.80	72.39	39.20
Malva sylvestris	Malvaceae	O	9.75	39.60	55.77	38.10
Circaea lutetiana	Onagraceae	N	17.34	36.60	58.19	37.60
Epilobium angustifolium	Onagraceae	O	53.19	33.80	55.32	35.60

Epilobium hirsutum	Onagraceae	O	37.54	21.30	71.85	37.60
Gaura lindheimeri	Onagraceae	N	35.38	15.10	93.88	36.00
Oenothera biennis	Onagraceae	N	27.96	23.10	78.38	37.50
Chelidonium majus	Papaveraceae	N	46.81	20.40	184.50	39.40
Papaver rhoeas	Papaveraceae	N	60.23	29.20	147.10	39.80
Plantago lanceolata	Plantaginaceae	N	19.68	23.80	99.71	38.50
Plantago media	Plantaginaceae	N	20.25	31.60	95.35	36.30
Lysimachia nummularia	Primulaceae	O	24.89	17.50	64.63	32.40
Lysimachia punctata	Primulaceae	O	22.92	9.50	68.65	33.10
Lysimachia vulgaris	Primulaceae	O	13.92	5.90	135.41	36.00
Anemone ranunculoides	Ranunculaceae	N	30.65	5.60	103.79	34.40
Aquilegia vulgaris	Ranunculaceae	N	44.41	19.50	168.78	36.50
Caltha palustris	Ranunculaceae	N	71.52	30.40	87.97	35.20
Clematis vitalba	Ranunculaceae	N	7.10	12.50	138.19	36.90
Ranunculus acris	Ranunculaceae	O	25.05	16.60	151.95	37.20
Ranunculus bulbosus	Ranunculaceae	O	28.93	14.10	85.32	37.40
Ranunculus lanuginosus	Ranunculaceae	O	36.34	22.20	86.39	38.40
Ranunculus repens	Ranunculaceae	O	32.25	21.00	57.51	37.20
Reseda lutea	Resedaceae	O	56.48	13.30	143.96	36.40
Agrimonia eupatoria	Rosaceae	N	41.62	5.90	131.36	37.40
Amelanchier lamarckii	Rosaceae	N	17.39	8.80	108.29	35.20
Filipendula ulmaria	Rosaceae	N	16.26	19.40	98.89	39.80
Potentilla anserina	Rosaceae	O	21.26	15.90	108.60	33.50
Potentilla reptans	Rosaceae	O	16.01	10.20	142.53	34.10
Prunus spinosa	Rosaceae	N	17.97	14.80	179.70	37.10
Rubus fruticosus	Rosaceae	N	5.28	17.10	217.14	36.50
Waldsteinia geoides	Rosaceae	N	38.19	6.50	158.31	36.40
Galium album	Rubiaceae	N	39.95	15.60	145.67	39.10
Salix cinerea	Salicaceae	O	33.41	38.60	122.32	38.00
Salix dasyclades	Salicaceae	O	24.17	37.10	154.88	40.20
Salix triandra	Salicaceae	O	25.25	25.80	182.59	38.00
Salix viminales	Salicaceae	O	26.36	27.70	161.21	40.20
Linaria vulgaris	Scrophulariaceae	N	55.82	10.70	185.12	37.10
Melampyrum pratense	Scrophulariaceae	N	96.47	5.40	156.42	36.30
Rhinanthus alectorolophus	Scrophulariaceae	N	73.29	15.90	182.90	37.90
Verbascum pulverulentum	Scrophulariaceae	N	42.22	11.50	211.54	40.60
Verbascum thapsus	Scrophulariaceae	N	44.09	10.60	148.33	38.70
Veronica chamaedrys	Scrophulariaceae	O	25.93	36.20	59.03	38.70
Solanum dulcamara	Solanaceae	N	39.89	21.10	248.86	39.00
Tilia cordata	Tiliaceae	N	35.07	19.10	91.80	34.80
Valeriana officinalis agg.	Valerianaceae	N	28.59	37.30	52.10	36.60
Viola reichenbachiana	Violaceae	N	28.39	9.00	142.43	34.00

5.4 Discussion

Our comparison of pollen amino acid composition showed that closely related species differ only slightly in their proportions of amino acids, suggesting that the profiles are a highly conserved trait. Compositional differences were most obvious between families and orders. Most plant species investigated contained the full spectrum of essential amino acids, albeit some in extremely small quantities. Earlier studies reported that tryptophan was lacking in several pollen species (Auclair and Jamieson 1948, Roulston and Cane 2000), partly for plants where tryptophane was detected only in trace amounts in our analysis. However, the strong quantitative limitation of tryptophane and occasionally methionine is evident and this limitation may be crucial for the development of bees or other pollen feeding insects.

Regarding pollen amino acid concentration on the family level (to compensate overrepresentation of closely related plants), our results are consistent with earlier findings of crude protein or nitrogen contents (Roulston et al. 2000): pollen known to be collected by oligoleges is neither more nor less nutritious than other pollen. On the species level oligolege pollen hosts contain significantly lower amounts of amino acids. These conflicting findings on family and species level may result from the latter being strongly dominated by common plant families, particularly Asteraceae and Lamiacae. Indeed some plants families are over-proportionally visited by oligoleges, whereas others do not host oligoleges at all. This suggests that evolutionary constraints may have played a major role in host-plant choice of oligoleges (Sedivy et al. 2008).

Host plants of oligoleges showed a poorer match to the ideal composition of essential pollen amino acids determined by De Groot (1953) than other plants. It may thus be possible that oligolectic bees are better adapted to a poorer nutritional quality of their host plants, among many other adaptations to their specific pollen sources. Accordingly, it has been hypothesised that specialist bee species may be more efficient in resource use than related generalists (Strickler 1979, Dobson and Peng 1997). Higher efficiency in pollen harvesting can be achieved through behavioural and morphological adaption (Müller and Bansac 2004). Examples are modification of mouth parts in oligolectic *Leioproctus* or a specialised hind leg brush in oligolectic *Megachile* species (Houston 1989, Müller and Bansac 2004). The evolution of such specialised pollen removal structures evolved several times independently in widely separated taxa, but is not restricted to oligolectic bees (Thorp 2000).

Nevertheless, Michez et al (2008) found some evidence that host switches occur more frequently to morphologically similar rather than closely-related plants.

Shorter handling time per flower and the ability of oligoleges to remove more pollen per flower than generalists was reported by Strickler (1979) and Cane and Payne (1988). These skills may lead to higher potential reproduction, since more pollen is collected for the brood cells per unit of handling time. However, bees do not adjust pollen provision based on the pollen's protein content. Roulston and Cane (2002) found the amount of pollen provision to predict larval performance only if, additionally to provision mass, protein content was considered. Besides, some evidence suggests that oligoleges are physiologically better adapted to digestion of their host plant pollen and can absorb the nutrients present in the pollen of their restricted food source more effectively than other bees (Dobson and Peng 1997, Praz et al. 2008). This might explain a choice of pollen species with lower total or essential amino acids. However, polylectic bees commonly collect monospecific pollen loads for nest provision (Westrich 1990) and thus also depend on the suitability of their particular provision. In brood cells containing pollen loads deficient in one or more essential amino acids, larvae would not be able to develop. Thus, it may not be surprising that polyleges select similar or even better pollen qualities. Adaptation to a certain pollen source may be associated with a cost: a decreased capability to digest other pollen types. Such costs are known to occur in host-specific herbivores (Strauss and Zangerl 2002) and were recently hypothesised for bees as well (Sedivy et al. 2008). While some studies demonstrated oligoleges to grow well on some non-host pollen (Bohart and Youssef 1976, Williams 2003), brood failure has been reported from other investigations (Guirguis and Brindley 1974, Praz et al. 2008). In some cases toxic compounds may be involved in specialist bees being able to cope better with some pollen species than others (Praz et al. 2008). To our knowledge no comparative approach of pollen toxins exists so far. If oligolectic bees specialised on pollen that is either deficient in amino acids or contains toxic compounds, this might have led to a competitive advantage in terms of the available pollen quantity and may explain why Asteraceae host large numbers of oligoleges but only few polyleges (Müller and Kuhlmann 2008). However, effective competitive avoidance has not been demonstrated so far. Most plant species visited by oligoleges are also regularly visited by polylectic bees and other insects, but this does not exclude the possibility of quantitative effects of competitive avoidance. Answering this question would require quantitative surveys of flower visitation and pollen removal rates.

6. Diversity and resource choice of flower visiting insects in relation to pollen nutritional quality and land use – synopsis and discussion

Biodiversity loss always is a matter of public concern. Yet, losses in pollinating insects are predestined to raise particular attention due to their potential effects on reproduction of wild flowers (Biesmeijer et al. 2006) and, above all, crop production and thus human welfare (Klein et al. 2003, Klein et al. 2007). Thus, albeit controversially discussed, the pollination crisis became a pervasive topic in ecology (Ghazoul 2005, Steffan-Dewenter et al. 2005).

Diverse communities of wild pollinators are stated to enhance stability, quality and quantity of pollination services (Lonsdorf et al. 2009). However, to assure this essential ecosystem service, wild pollinator assemblages rely on appropriate foraging resources as well as nesting sites within foraging distance of floral patches.

The goal of my thesis was to examine how and via which pathways land use affects plant-pollinator communities. We investigated their diversity in relation to different land-use intensities and management strategies. Contrasting results between different pollinator groups demanded to illuminate the relationship between species niche properties and vulnerability to disturbance. We analyzed species response in relation to specialization and demonstrated that species-specific plant and pollinator responses to land use may be predicted by the land-use response of each species' partners when relative interaction strength is considered. Our findings confirm that ecological networks suit to predict natural community responses to disturbance and possible secondary extinctions. As specialization in pollinators potentially is associated with high costs, we explored if it on the other hand coincides with higher foraging efficiency and investigated if resource choice in pollinators is influenced by pollen nutritional quality.

6.1 Land-use effects on plant communities

Frequent mowing, grazing and fertilization are known to have profound effects on plant species richness and functional diversity (Proulx and Mazumder 1998, Maskell et al. 2010). Thus, floral composition and species richness of grasslands partly mirror their management regime (Fenner and Palmer 1998). Our comparison between meadows used at high or low land-use intensities revealed crucial differences in plant species

composition even between barely varying management types, with species overlaps of less than 43 per cent (Chapter 2). Plant species richness and diversity declined with increasing land-use intensity (Chapter 2-3). Our results showed that even gradual differences in management intensity, particularly increases in mowing frequency and fertilization, lead to changes in species composition and losses in plant diversity (Chapter 2, 4). Thus, we confirmed former studies detecting decreases in flower diversity with increasing fertilizer application and mowing frequency (Mountford et al. 1993, Socher et al. 2012). Nonetheless, a more detailed look at the isolated effects of different land-use components revealed differing trends between Exploratories, i.e. results cannot be transferred without further ado between regions (Chapter 4). Considering the importance of regional contexts, similar findings were reported from other studies conducted within the framework of the Biodiversity Exploratories project (e.g. Blüthgen et al. 2012, Socher et al. 2012, Socher et al. 2013).

The average land-use response of a plant species was predicted by the weighted response of its pollinators, and did not differ with plant specialization (Chapter 3, 4) or between self-compatible and self-incompatible plants (Chapter 3). This is consistent with a review by Aizen et al. (2002) who reported that neither breeding system nor specialization determined plant susceptibility to disturbance. Albeit average specialization in plants was very high, responses of plants to pollinator fate were less pronounced than responses of pollinators to plant fate, i.e. resource loss (Chapter 3, 4). This may be due to the fact that many plant species are capable of vegetative reproduction or do not depend obligatorily on out-crossing (Klotz et al. 2002). Nevertheless, land-use intensification reduced taxonomic breadth of some pollinator groups such as bees and butterflies (Chapter 2-4). This most probably causes a reduction in the functional diversity of pollinators, which could conversely affect plant species richness and functional diversity (Klein et al. 2003, Hoehn et al. 2008). While plant reproductive fitness may be at risk over longer time spans, the immediate effects on the fitness and local distribution of pollinators may be more severe when their foraging resources become unavailable (Biesmeijer et al. 2006, Goulson et al. 2008, Bommarco et al. 2010).

Nevertheless, plant responses to land-use intensity were related to relative species abundance with rare plants showing a stronger decline with increasing land use than more abundant ones (Chapter 3). Additionally, conversely with other studies (Ebeling et al. 2008), the total number of visits to a plant species was positively related to overall

floral abundance in terms of flowering area (Chapter 2). This implies that rare plants may suffer disproportionately from a decrease in pollinator diversity and abundance. A clear plurality of studies showed that pollination and reproductive success decrease in sparse and sometimes also in small populations, particularly in self-incompatible plant species (Silander 1978, Jennerston 1988, Kunin 1992, Agren 1996, Knight 2003, Aguilar and Galetto 2004, Hirayama et al. 2007, Kolb 2008). Still, competition for a limited number of pollinators may lead to reductions in per capita pollinator visits and pollen limitation in large or very dense populations (Cambell and Husband 2007, Spigler and Chang 2009). Reductions in reproductive output in terms of seed set may result from declines in either pollination quantity or quality of visits. As large plant populations and high flower densities tend to attract higher numbers of pollinators (Cheptou and Avendano 2006, Bernhardt et al. 2008) pollen flow within the population is secured even if per capita visitation might be lower than in some smaller populations. Moreover, visitors to dense populations are expected to be more flower constant, thus increasing the chance of intra-specific pollen transfer (Kunin 1997). In contrast, in small populations beneath negative effects from inter-specific pollen transfer higher rates of inbreeding may lead to difficulties due to genetic reasons (lowered population viability) and increase local extinction risk (Ellstrand and Elam 1993, Byers 1995, Waites and Agren 2004). If plant reproductive success decreases with decreasing population size, rareness rather than specialization may determine plant fate in relation to pollination and land-use intensification.

6.2 Consequences from land use for mutualistic plant-pollinator interactions

Agricultural management is also a major factor determining diversity and persistence of faunal richness in anthropogenic landscapes. In contrast to plants, in pollinators, responses to land-use intensity were independent of pollinator abundance (Chapter 3) and seem to depend on species-specific pollinator traits (Chapter 2-4). We found that pollinator composition corresponded to floral composition (Chapter 3) and that overall species composition of pollinators differed considerably between meadows varying in mowing frequency and fertilization intensity (Chapter 2). However, neither total pollinator species richness nor abundance or diversity was correlated negatively to land-use intensity (Chapter 2-4). When regarded in isolation, composition of bees and butterflies differed considerably between meadow types, whereas the other pollinator

groups did not show significant differences related to management (Chapter 2). In spite of this, with increasing land-use intensity the proportional abundance and species richness of dipterans, especially syrphids, mostly increased, whereas it mostly decreased in bees and other hymenopterans as well as in butterflies and beetles (Chapter 2-4). These results highlight that different pollinator-groups respond differently to disturbance. They are in line with earlier studies indicating opposing trends in the responses of wild bees and syrphids to agricultural change and landscape structure (Biesmeijer et al. 2006, Jauker et al. 2009). Moreover, they point to the fact that investigation of species biodiversity alone may not detect biotic homogenization e.g. losses in functional diversity (Filippi-Codaccioni et al. 2010).

The number of visitor individuals per meadow varied independently of its total flowering area. Thus, in our study, total flower density was not the vital factor determining overall pollinator abundance. Nevertheless, visitation and flowering area of each plant species within each network correlated positively (Chapter 2). Within a grassland plot, a plant species with a high density, e.g. a large flowering area, received more visits in total. This indicates that flower density plays a role for the distribution of visitors within a site. Furthermore, it implies that rare plant species may receive fewer visits than abundant ones, at least on a per site basis, which beneath effects outlined above may lead to poor seed set, high selfing rates, and inbreeding depression (Fischer and Matthies 1997, Spira 2001). Considering that rare plants in our study declined disproportionately with increasing land-use intensity, besides direct effects from land use, pollinator response to flowering area may explain why these plants are exceptionally prone to disturbance (Chapter 3).

In addition to floral abundance, pollinator abundance, composition and diversity may be triggered by floral diversity and species-specific plant preferences (Tudor et al. 2004, Ebeling et al. 2008, Kleijn and Raemakers 2008, Fründ et al. 2010). This was also reflected by our results: a decline in plant species frequently visited by a pollinator often went along with a decline in this pollinator (Chapter 3, 4). Furthermore, pollinator species composition depended on plant species composition and in some pollinator guilds on land-use type (Chapter 2).

Although land-use type explained only a small percentage of the total compositional variation in pollinators (Chapter 2), land use may affect pollinators directly e.g. via disruption of life cycles (Johst et al. 2006) or supply of appropriate nesting resources

(Potts et al. 2005). Such direct effects are known to add on indirect effects via flower composition and availability, landscape context and availability of larval habitats. For example, parasitic wasps depend on the local abundance of hosts (Steffan-Dewenter 2003) and in many bees and beetles abundance depends on certain habitats and landscape structures as well as specific larval or nesting sites (Gathmann and Tscharntke 2002). On the other hand, generalized flower visitors like most syrphids and other dipterans are not restricted to certain landscape structures and may profit from diverse larval habitats within their foraging range (Jauker et al. 2009). In syrphids females can spread into landscapes progressively, alternating between oviposition and feeding. Contrarily, bees collect pollen and nectar for their offspring and repeatedly need to return to the brood cells after foraging, especially small and less mobile species may be restricted to grasslands offering nesting sites. Such sites may then be characterized by higher bee diversity and abundance. While high grazing intensity similar to mowing may destroy larval habitats, in our study such negative aspects were outweighed by positive ones. The positive effects of grazing intensity we partly observed in bees, butterflies and beetles (Chapter 4) may be related to the fact that grazing leads to high sward heterogeneity offering a variety of microclimates, produces nesting sites of bare soil for ground-nesting insects and fosters important pollen and nectar resources as well as larval food plants for a high variety of pollinators (Beil and Kratochwil 2004).

Unlike grazing, mowing leads to a frequent unselective removal of food resources and a rather homogeneus sward structure. Moreover, it goes along with changes in plant composition, may destroy larval habitats and is detrimental to most immobile larvae. Therefore negative correlations between mowing intensity and responses in some pollinator guilds may be stronger than responses to fertilization intensity which in real world landscapes is highly correlated to mowing frequency and seemed to influence pollinators rather indirectly via changes in plant diversity and composition (Chapter 4).

In our studies plant-pollinator networks proved to be highly structured. The level of network specialization H_2' was relatively similar for all flower-visitor networks recorded and yielded values around H_2' = 0.60, which are also typical of other plant-pollinator associations (Blüthgen et al. 2007). Thus, most networks were highly structured, deviating significantly from random associations (Chapter 2-4).

The level of species specialization d_i' was highest for bees, intermediate for butterflies, beetles and hymenopterans excluding bees, and lowest for syrphids and other dipterans.

The overall ranking proved to be stable between years and showed mostly similar trends between different regions (Chapter 2-4).

Specialized pollinators such as oligolectic bees are often expected to be more prone to disturbance and thus more vulnerable to ecosystem change (Colwell et al. 2012). This is recognized as the cost of specialization and was reinforced by our results (Chapter 3 and 4). Dipteran flower visitors were least specialized and showed little changes in species composition and an increase in abundance rather than a decrease related to land-use intensity. More specialized pollinators e.g. butterflies and bees showed compositional differences between management types and mostly decreased with increasing land-use intensity (Chapter 2-4). This corresponds to investigations on bumblebees, butterflies and beetles which demonstrated that many specialized species are of conservation concern and have undergone a considerable decline in the last decades (Kotze and O´Hara 2003, Tudor et al. 2004, Kleijn and Raemakers 2008)

Beneath the response of the plant species associated with a certain pollinator, pollinator response to land use was significantly influenced by pollinator specialization and taxonomic identity (Chapter 2-4). In rather specialized species responses to land-use intensity were more strongly driven by the responses of their preferred plants than in more generalized pollinators (Chapter 3, 4). Accordingly, on average specialized pollinator taxa reflected the land-use response of the plant species they visited in their own relative abundance. In contrast, syrphids and other dipterans seemed to respond to land-use changes more independently from associated plants (Chapter 3). Nevertheless, the identified positive effects of mowing intensity on syrphids and other dipterans could be attributed to the observation that intensively used meadows offer a higher abundance of easily exploitable flowers like Asteraceae and Apidaceae which are readily visited by dipterans (Chapter 2, 4) which feed preferably on shallow flowers offering a lot of pollen (Kevan and Baker 1983). Thus, our results are not only in line with the theory that specialist species with narrow ecological niches are more susceptible to rapidly changing environmental conditions, but also confirm that specialization represents a risk that renders species more vulnerable to co-extinction (McKinney 1997, Vázquez and Simberloff 2002, Winfree et al. 2007, Aizen et al. 2012, Pocock et al. 2012).

Differences in plant species composition together with high specialization may explain the considerable differences in pollinator composition and functional diversity between differently managed grasslands. Furthermore, diversity declines in specialist species

suggest that they rely more heavily on their preferred plant species, while diversity and composition of dipterans was not consistently affected by land use in our study, corresponding to their low degree of flower specialization.

The results from my thesis suggest that land-use intensification primarily triggers losses in flower diversity and changes in composition, which then may lead to non-random and resource-mediated declines in certain pollinators. Although land-use responses of the pollinators visiting a plant species may also influence plant abundance, this effect is weaker. While overall pollinator diversity is not significantly affected, pollinator species composition changes considerably (Chapter 2-4). Land-use intensification has a disproportionate impact on the abundance of more specialized pollinators, and on the abundance of rare plant species (Chapter 3). Overall, species responses in plants and pollinators were most strongly pronounced in relation to the intensification of mowing which thus seems to be a major factor influencing the composition of plant-pollinator networks (Chapter 4).

6.3 Pollen nutritional quality in relation to specialization in pollinators

Pollen amino acid profiles suggest that plants differ considerably in the concentration and composition of pollen proteins and free amino acids (Chapter 5). In butterflies and honey bees a preference for pollen and nectar that contains high concentrations of amino acids was found (Alm et al. 1990, Erhardt and Baker 1990, Cook et al. 2003). Furthermore, the ingestion of pollen or nectar rich in amino acids is known to promote reproductive fitness in butterflies (Lanza et al. 1997, Mevi-Schutz and Erhardt 2005) and body size in bees (Roulston and Cane 2002, Tasei and Aupinel 2008, Quezada-Euan et al. 2011). Thus, visitation rate, visitor diversity and specialization of pollinators may increase with the quality of pollen plants offer.

We aimed to find out whether amino acid composition affects host plant selection of oligolectic bees. Thus, we compared amino acid concentration, homogeneity of composition and deviation from the ideal composition of essential amino acids between pollen known to be collected by oligoleges and pollen only collected by polylectic bees. The composition of amino acids varied strongly among plant species, but cognate plant species displayed similar composition (Chapter 5). This confirmed earlier work by Roulston et al. (2000) where protein concentrations were found to be highly conserved

within plant genera and families. If amino acid content influences flower visitation, flower visitors, above all pollen specialists, are hypothesized to select for plants rich in amino acids (Roulston et al. 2000). Surprisingly, the concentration of free- and protein-bound amino acids – also of the essential ones – is significantly lower in pollen sources used by oligolectic bees than in other pollen sources (Chapter 5). Moreover, pollen sources of oligoleges deviated more strongly from the ideal composition of essential amino acids as determined for honey bees (De Groot 1953) than pollen sources not hosting oligolectic bees.

This leads to the assumption that competitive avoidance or in other words an advantage in terms of the available pollen quantity might have led to oligolectic bees being specialized on pollen that is rather deficient in amino acids (Chapter 5). Though it still needs to be tested in detail, a recent study considering Asteraceae and their flower visitors revealed that plants hosting oligoleges are barely visited by generalists (Müller and Kuhlmann 2008).

However, benefits of specialization may also result from more efficient handling of host flowers (Strickler 1979), more effective pollen collection due to specific pollen-harvesting structures (Müller and Bansac 2004), more proficient digestion (Dobson and Peng 1997) and specialized detoxification abilities (Williams 2003).

6.4 Conclusions

Land-use intensification sets off losses in flower diversity, which leads to resource-mediated declines in pollinator species. While the mean land-use response of the pollinators visiting a plant species also influenced its abundance, this effect is weaker. Network analyses provide a valuable tool for characterizing mutualism in a community context and may be used to predict community responses to disturbance and possible consequences of species loss. Our findings emphasize how systems based on mutualism may undergo severe transformation due to land-use intensification. Mutual specialization could offer an explanation for the accelerating parallel declines observed in plants and pollinators.

Literature

Adler, P. B., E. W. Seabloom, E. T. Borer, H. Hillebrand, Y. Hautier, A. Hector, and W. S. Harpole. 2011. Productivity is a poor predictor of plant species richness. Science **333**:1750-1753.

Agren, J. 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb Lythrum salicaria. Ecology **77**:1779-1790.

Aguilar, R., L. Ashworth, L. Galetto, and M. A. Aizen. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecology Letters **9**:968-980.

Aguilar, R. and L. Galetto. 2004. Effects of forest fragmentation on male and female reproductive success in *Cestrum parqui* (Solanaceae). Oecologia **138**:513-520.

Aizen, M. A., L. Ashworth, and L. Galetto. 2002. Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? Journal of Vegetation Science **13**:885-892.

Aizen, M. A. and P. Feinsinger. 2003. Bees not to be? Responses of insect pollinator faunas and flower pollination to habitat fragmentation. Pages 111-129 *in* G. Bradshaw and P. Marquet, editors. How Landscapes Change. Springer Berlin Heidelberg.

Aizen, M. A. and L. D. Harder. 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Current Biology **19**:1-4.

Aizen, M. A., M. Sabatiano, and J. M. Tylianakis. 2012. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. Science **335**:1486-1489.

Allen-Wardell, G., P. Bernhardt, R. Bitner, A. Burquez, S. Buchmann, J. Cane, P. A. Cox, V. Dalton, P. Feinsinger, M. Ingram, D. Inouye, C. E. Jones, K. Kennedy, P. Kevan, H. Koopowitz, R. Medellin, S. Medellin-Morales, and G. P. Nabhan. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conservation Biology **12**:8-17.

Alm, J., T. E. Ohnmeiss, J. Lanza, and L. Vriesenga. 1990. Preference of cabbage white butterflies and honey bees for nectar that contains amino acids. Oecologia **84**:53-57.

Armbruster, W. S. and B. G. Baldwin. 1998. Switch from specialized to generalized pollination. Nature **394**:632.

Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses, and global change. Annual Review of Environment and Resources **29**:261-299.

Auclair, J. L. and C. A. Jamieson. 1948. Qualitative analysis of amino acids in pollen collected by bees. Science **108**:357-358.

Barmaz, S., S. G. Potts, and M. Vighi. 2010. A novel method for assessing risks to pollinators from plant protection products using honeybees as a model species. Ecotoxicology **19**:1347-1359.

Barmaz, S., C. Vaj, A. Ippolito, and M. Vighi. 2012. Exposure of pollinators to plant protection products. Ecotoxicology **21**:2177-2185.

Begon, M., J. L. Harper, and C. R. Townsend. 1990. Ecology: individuals, populations and communities. 2 edition. Blackwell Scientific Publications, Boston.

Beil, M. and A. Kratochwil. 2004. Zur Ressourcennutzung von Wildbienen (Hymenoptera, Apoidea) in beweideten und unbeweideten Sand-ökosystemen. Beweidung und Restitution als Chancen für den Naturschutz:179-189.

Bellard, C., C. Bertelsmeier, P. W. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters **15**:365-377.

Benadi, G., N. Blüthgen, T. Hovestadt, and H. J. Poethke. 2012. Population dynamics of interacting plant and pollinator communities: stability reconsidered. American Naturalist **179**:157-168.

Bernhardt, C. E., R. J. Mitchell, and H. J. Michaels. 2008. Effects of population size and density on pollinator visitation, pollinator behavior, and pollen tube abundance in *Lupinus perennis*. International Journal of plant science **169**:944-953.

Biesmeijer, J. C., S. P. M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, and W. E. Kunin. 2006. Parallel declines in pollinators and insect pollinated plants in Britain and the Netherlands. Science **313**:351-354.

Binot-Hafke, M., S. Balzer, N. Becker, H. Gruttke, H. Haupt, N. Hofbauer, G. Ludwig, G. Matzke-Hajek, and M. Strauch, editors. 2011. Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands. Band 3: Wirbellose (Teil 1). Bundesamt für Naturschutz, Bonn-Bad Godesberg.

Binot, M., R. Bless, P. Boye, H. Gruttke, and P. Pretscher, editors. 1998. Rote Liste gefährdeter Tiere Deutschlands. Bundesamt für Naturschutz, Bonn-Bad Godesberg.

Blüthgen, N. 2010. Why network analysis is often disconnected from community ecology: A critique and an ecologist´s guide. Basic and Applied Ecology **11**:185-195.

Blüthgen, N., C. Dormann, F. Alt, S. Boch, V. Klaus, T. Kleinebecker, S. Gockel, J. Nieschulze, S. Renner, U. Schumacher, K. Birkhofer, F. Buscot, M. Fischer, A. Hemp, N. Hölzel, E. K. V. Kalko, K. E. Linsenmair, Y. Oelmann, D. Prati, C. Rothenwöhrer, C. Scherber, I. Schöning, E.-D. Schulze, T. Tscharntke, C. N. Weiner, K. Wells, and W. W. Weisser. 2012. A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. Basic and Applied Ecology **13**:207-220.

Blüthgen, N. and K. Fiedler. 2004. Preferences for sugars and amino acids and their conditionality in a diverse nectar-feeding ant community. Journal of Animal Ecology **73**:155-166.

Blüthgen, N., J. Fründ, D. P. Vázquez, and F. Menzel. 2008. What do interaction network metrics tell us about specilization and biological traits? Ecology **89**:3387-3399.

Blüthgen, N. and A.-M. Klein. 2011. Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. Basic and Applied Ecology **12**:282-291.

Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. Measuring specialization in species interaction networks. BMC Ecology **6**:9.

Blüthgen, N., F. Menzel, T. Hovestadt, B. Fiala, and N. Blüthgen. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. Current Biology **17**:341-346.

Bohart, G. E. and N. N. Youssef. 1976. The biology and behavior of *Evylaeus galpinsiae* Cockerell (Hymenoptera: Halictidae). Wasmann Journal of Biology **34**:185-234.

Bommarco, R., J. C. Biesmeijer, B. Meyer, S. G. Potts, J. Pöyry, S. P. M. Roberts, I. Steffan-Dewenter, and E. Öckinger. 2010. Dispersal capacity and diet breath modify the response of wild bees to habitat loss. Proceedings of the Royal Society Biological Sciences Series B **277**:2075-2082.

Börschig, C., A.-M. Klein, H. von Wehrden, and J. Krauss. 2013. Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. Basic and Applied Ecology **14**:547-554.

Bradford, M. A., T. H. Jones, B. R. D:, H. I. J. Black, B. Boag, M. Bonkowski, R. Cook, T. Eggers, A. C. Gange, S. J. Grayston, E. Kandeler, A. E. McCaig, J. E. Newington, J. I. Prosser, H. Setala, P. L. Staddon, G. M. Tordoff, D. Tscherko, and J. H. Lawton. 2002. Impacts of soil faunal community composition on model grassland ecosystems. Science **298**:615-618.

Brittain, C. and S. G. Potts. 2011. The potential impacts of insecticides on the life-history traits of bees and the consequences for pollination. Basic and Applied Ecology **12**:321-331.

Budde, J., A. Reckert, F. Sporer, M. Wink, T. Eltz, and K. Lunau. 2004. Beiträge zur Evolution der Oligolektie bei solitären Bienen der Gattung *Andrena*. Entomologie Heute **16**:191-200.

Bulan, C. A. and G. W. Barrett. 1971. The effects of two acute stresses on the arthropod component of an experimental grassland ecosystem. Ecology **52**:597-605.

Burkle, L. and R. E. Irwin. 2009. The importance of interannual variation and bottom-up nitrogen enrichment for plant-pollinator networks. Oikos **118**:1816-1829.

Burkle, L. A. and R. E. Irwin. 2010. Beyond biomass: measuring the effects of community level nitrogen enrichment on floral traits, pollinator vsitation and plant reproduction. Journal of Ecology **98**:705-717.

Butchart, S. H. M., M. Walpole, B. Collen, A. van Strien, J. Scharlemann, R. E. A. Almond, J. E. M. Baillie, B. Bomhard, C. Brown, J. Bruno, K. E. Carpenter, G. M. Carr, J. Chanson, A. M. Chenery, J. Csirke, N. C. Davidson, F. Dentener, M. Foster, A. Galli, J. N. Galloway, P. Genovesi, R. D. Gregory, M. Hockings, V. Kapos, J.-F. Lamarque, F. Leverington, J. Loh, M. A. McGeoch, L. McRae, A. Minasyan, M. Hernández Morcillo, T. E. E. Oldfield, D. Pauly, S. Quader, C. Revenga, J. R. Sauer, B. Skolnik, D. Spear, D. Stanwell-Smith, S. N. Stuart, A. Symes, M. Tierney, T. D. Tyrrell, J.-C. Vié, and R. Watson. 2010. Global biodiversity: Indicators of recent declines. Science **328**:1164-1168.

Byers, D. L. 1995. Pollen quantity and quality as explanations for low seed set in small populations exemplified by *Eupatorium* (Asteraceae). American Journal of Botany **82**:1000-1006.

Cambell, L. G. and B. C. Husband. 2007. Small populations are mate-poor but pollinator-rich in a rare, self-incompatible plant, *Hymenoxys herbaceae* (Asteraceae). New Phytologist **174**:915-925.

Cane, J. H. and J. A. Payne. 1988. Foraging ecology of the bee *Habropoda laboriosa* (Hymenoptera: Anthophoridae),an oligolege of blueberries (Ericaceae: *Vaccinium*) in the southeastern United States. Annals of the Entomological Society of America **81**:419-427.

Cane, J. H. and S. D. Sipes. 2006. Characterizing floral specialization by bees: Analytical methods and a revised lexicon for oligolecty. Pages 99-122 *in* N. M. Waser and J. Ollerton, editors. Specialization and Generalization in Plant-Pollinator Interactions. University of Chicago Press, Chicago.

Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of Science **104**:18123-18128.

Chacoff, N. P., D. P. Vázquez, S. B. Lomáscolo, E. L. Stevani, J. Dorado, and B. Padrón. 2012. Evaluating sampling completeness in a desert plant-pollinator network. Journal of Animal Ecology **81**:190-200.

Cheptou, P.-O. and L. G. Avendano. 2006. Pollination processes and the Allee effect in highly fragmented populations: consequences for the mating system in urban environments. New Phytologist **172**:774-783.

Clavel, J., R. Julliard, and V. Devictor. 2010. Worldwide decline of specialist species: toward a global functional homogenization? Frontiers in ecology and the environment **9**:222-228.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science **280**:745-747.

Colwell, R. K., R. R. Dunn, and N. C. Harris. 2012. Coextinction and persistence of dependent species in a changing world. Annual Review of Ecology, Evolution and Systematics **43**:183-203.

Cook, S. M., C. S. Awmack, D. A. Murray, and I. H. Williams. 2003. Are honey bees' foraging preferences affected by pollen amino acid composition? Ecological Entomology **28**:622-627.

Crane, E. and P. Walker. 1983. The impact of pest management on bees and pollination. International Bee research Association, London.

Crawley, M. J., A. E. Johnston, J. Silvertown, M. Dodd, C. de Mazancourt, M. S. Heard, D. F. Henman, and G. R. Edwards. 2005. Determinants of species richness in the Park Grass experiment. American Naturalist **165**:179-192.

Cunningham, S. A. 2000. Depressed pollination in habitat fragments causes low fruit set. Proceedings of the Royal Society London Series B **267**:1149-1152.

Daily, G. C., editor. 1997. Nature's services. Island press, Washington.

Danforth, B. N., L. Conway, and S. Ji. 2003. Phylogeny of eusocial *Lasioglossum* reveals multiple losses of eusociality within a primitively eusocial clade of bees (Hymenoptera: Halictidae). Systematic Biology **52**:23-36.

Day, S., R. Beyer, A. Mercer, and S. Ogden. 1990. The nutrient composition of honeybee-collected pollen in Otago, New Zealand. Journal of Apicultural Research **29**:138-146.

De Groot, A. P. 1952. Amino acid requirements for the growth of the honeybee (*Apis mellifera* L.). Experentia **8**:1992-1994.

De Groot, A. P. 1953. Protein and amino acid requirements of the honey bee (*Apis mellifera* L.). Physiologia Comparata et Oecologia **3**:197-285.

Den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheoretica **18**:165-194.

Desneux, N., A. Decourtye, and J.-M. Delpuech. 2007. The sublethal effects of pesticides on beneficial arthropods. Annual Review of Entomology **52**:81-106.

Dicks, L. V., S. A. Corbet, and R. F. Pywell. 2002. Compartmentalization in plant-insect flower visitor webs. Journal of Animal Ecology **71**:32-43.

Dobson, H. E. M. and Y.-S. Peng. 1997. Digestion of pollen components by larvae of the flower-specialist bee *Chelostoma florisomne* (Hymenoptera: Megachilidae). Journal of Insect Physiology **43**:89-100.

Dorado, J., D. P. Vázquez, E. Stevani, and N. Chacoff. 2009. Rareness ans specializaion in plant-pollinator networks. Ecology **92**:19-25.

Dormann, C. F., J. Fründ, N. Blüthgen, and B. Gruber. 2009. Indices, graphs and null models: analysing bipartide ecological networks. The Open Ecology Journal **2**:7-24.

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Food-web structure and network theory: the role of connectance and size. Proceedings of the National Academy of Sciences of the United States of America **99**:12917-12922.

Duraiappah, A. and S. Naeem. 2005. Ecosystems and human well-being: biodiversity ynthesis. World Resources Institute, Washington DC.

Ebeling, A., A.-M. Klein, J. Schumacher, W. W. Weisser, and T. Tscharntke. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos **117**:1808-1815.

Ehrlich, P. R. and E. O. Wilson. 1991. Biodiversity studies: science and policy. Science **253**:758-762.

Ellstrand, N. C. and D. R. Elam. 1993. Population genetic consequences of small population size: implications for plant conservation. Annual Review of Ecology and Systematics **24**:217-242.

Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in ecology and the environment **1**:488-494.

Erhardt, A. and I. Baker. 1990. Pollen amino acids an additional diet for a nectar feeding butterfly. Plant Systematics & Evolution **169**:111-121.

Erhardt, A. and H. P. Rusterholz. 1998. Do peacock butterflies (*Inachis io* L.) detect and prefer nectar amino acids and other nitrogenous compounds? Oecologia **117**:536-542.

Fenner, M. and L. Palmer. 1998. Grassland management to promote diversity: creation of a patchy sward by mowing and fertiliser regimes. Field studies **9**:313-324.

Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash, and J. D. Thomson. 2004. Pollination syndromes and floral specialization. Annual Review of Ecology, Evolution and Systematics **35**:375-403.

Filippi-Codaccioni, O., V. Devictor, Y. Bas, and R. Julliard. 2010. Toward more concern for specialisation and less species diversity in conserving farmland biodiversity. Biological conservation **143**:1493-1500.

Fischer, M., O. Bossdorf, S. Gockel, F. Hänsel, A. Hemp, D. Hessenmöller, G. Korte, J. Nieschulze, S. Pfeiffer, D. Prati, S. Renner, I. Schöning, U. Schumacher, K. Wells, F. Buscot, E. Kalko, K. E. Linsenmair, E.-D. Schulze, and W. W. Weisser. 2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. Basic and Applied Ecology **11**:473-485.

Fischer, M. and D. Matthies. 1997. Mating structure and inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (Gentianaceae). American Journal of Botany **84**:1685.

Fontaine, C., I. Dajoz, J. Meriguet, and M. Loreau. 2006. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. PLoS Biology **4**:e1.

Fründ, J., K. E. Linsenmair, and N. Blüthgen. 2010. Pollinator diversity and specialization in relation to flower diversity. Oikos **119**:1581-1590.

Gathmann, A. and T. Tscharntke. 2002. Foraging ranges of solitary bees. Journal of Animal Ecology **71**:757-764.

Ghazoul, J. 2005. Buzziness as usual? Questioning the global pollination crisis. Trends in Ecology and Evolution **20**:367-373.

Ghazoul, J. 2006. Floral diversity and the facilitation of pollination. Journal of Ecology **94**:295-304.

Gibson, C. W. D., V. K. Brown, L. Losito, and G. C. McGavin. 1992. The response of invertebrate assemblies to grazing. Ecography **15**:166–176.

Gilbert, L. E. 1972. Pollen feeding and reproductive biology of *Heliconius* butterflies. Proceedings of the National Academy of Science **69**:1403-1407.

Gotelli, N. J. and G. L. Entsminger. 2009. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. http://garyentsminger.com/ecosim.htm.

Goulson, D. 2003. Effects of introduced bees on native ecosystems. Annual Review of Ecology, Evolution and Systematics **34**:1-26.

Goulson, D. and B. Darvill. 2004. Niche overlap and diet breadth in bumblebees: are rare species more specialized in their choice of flowers? Apidologie **35**:55-63.

Goulson, D., G. C. Lye, and B. Darvill. 2008. The decline and conservation of bumblebees. Annual Review of Entomology **53**:191-208.

Grime, J. 1973. Competitive exclusion in herbaceous vegetation. Nature **242**:344-347.

Grindeland, J. M., N. Sletvold, and R. A. Ims. 2005. Effects of floral display size and plant density on pollinator visitation rate in a natural population of *Digitalis purpurea*. Functional Ecology **19**:383-390.

Guirguis, G. N. and W. A. Brindley. 1974. Insecticide susceptibility and response to selected pollens of larval alfalfa leafcutting bees, *Megachile pacifica* (Panzer) (Hymenoptera: Megachilidae). Environmental Entomology **3**:691-694.

Gullan, P. J. and P. S. Cranston. 2005. The Insects: An Outline of Entomology. 3 edition. Blackwell Publishing, Oxford, UK.

Haddad, N. M., J. Haarstad, and D. Tilman. 2000. The effects of long-term nitrogen loading on grassland insect communities. Oecologia **124**:73-84.

Hansson, M. and H. Fogelfors. 2000. Management of a semi-natural grassland: Results from a 15-year-old experiment in Southern Sweden. Journal of Vegetation Science **11**:31-38.

Hassan, R., R. Scholes, and N. Ash, editors. 2005. Ecosystems and human well-being: Current state and trends. Island Press, Washington DC.

Hautier, Y., P. A. Niklaus, and A. Hector. 2009. Competition for light causes plant biodiversity loss after eutrophication. Science **324**:636-638.

Hawkins, B. and E. Porter. 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. The American Naturalist **161**:40-49.

Hector, A. and R. Bagchi. 2007. Biodiversity and ecosystem multifunctionality. Nature **448**:188-190.

Hector, A., B. Schmid, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. A. Finn, H. Freitas, P. S. Giller, J. Good, R. Harris, P. Högberg, K. Huss-Danell, J. Joshi, A. Jumpponen, C. Körner, P. W. Leadley, M. Loreau, A. Minns, C. P. H. Mulder, G. O'Donovan, S. J. Otway, J. S. Pereira, A. Prinz, D. J. Read, M. Scherer-Lorenzen, E.-D. Schulze, A.-S. D. Siamantziouras, E. M. Spehn, A. C. Terry, A. Y. Troumbis, F. I. Woodward, S. Yachi, and J. H. Lawton. 1999. Plant diversity and productivity experiments in European grasslands. Science **286**:1123-1127.

Hirayama, K., K. Ishida, S. Setsuko, and N. Tomaru. 2007. Reduced seed production, inbreeding, and pollen shortage in a small population of a threatened tree, *Magnolia stellata*. Biological conservation **136**:315-323.

Hoehn, P., T. Tscharntke, J. M. Tylianakis, and I. Steffan-Dewenter. 2008. Functional group diversity of bee pollinators increases crop yield. Proceedings of the Royal Society Biological Sciences Series B **275**:2283-2291.

Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. Proceedings of the National Academy of Science **106**:19659–19665.

Hooper, D. U., F. S. Chapin, A. Ewel, A. Hector, P. Inchausti, J. H. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current kwoledge. Ecological Monographs **75**:3-35.

Houston, T. F. 1989. *Leioproctus* bees associated with Western Australian smoke bushes (*Conospermum spp.*) and their adaptations for foraging and concealment (Hymenoptera: Colletidae: Paracolletini). Records of the Western Australian Museum **14**:275-292.

James, A., J. W. Pitchford, and M. J. Plank. 2012. Distangeling nestedness from models of ecological complexity. Nature **487**:227-230.

Jauker, F., B. Bondarenko, H. C. Becker, and I. Steffan-Dewenter. 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agricultural and Forest Entomology **14**:81-87.

Jauker, F., T. Diekötter, F. Schwarzbach, and V. Wolters. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecology **24**:547-555.

Jennerston, O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): Effects of habitat fragmentation on visitation and seed set. Conservation Biology **2**:359-366

Johansen, C. A. 1977. Pesticides and pollinators. Annual Review of Entomology **22**:177-192.
Johnson, S. D. and K. E. Steiner. 2000. Generalization versus specialization in plant pollination systems. Trends in Ecology and Evolution **15**:140-143.
Johst, K., M. Drechsler, and J. Settele. 2006. Influence of mowing on the persistence of two endangered large butterfly species. Journal of Applied Ecology **43**:333-342.
Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. American Naturalist **129**:657-677.
Junker, R. and N. Blüthgen. 2010. Floral scents repel facultative flower visitors, but attract obligate ones. Annals of Botany **105**:777-782.
Kaiser-Bunbury, C. N., S. Muff, J. Memmott, C. B. Müller, and A. Caflisch. 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. Ecology Letters **13**:442-452.
Kalisz, S., D. W. Vogler, and K. Hanley. 2004. Context-dependent autonomous self-fertilization yields reproductive assurance and mixed mating. Nature **430**:884-887.
Keitt, T. H. 2009. Habitat conversion, extinction thresholds,and pollination services in agroecosystems. Ecological Applications **19**:1561-1573.
Kevan, P. G. and H. G. Baker. 1983. Insects as flower visitors and pollinators. Annual Review of Entomology **28**:407-453.
Kevan, P. G. and T. P. Phillips. 2001. The economic impacts of pollinator declines: an approach to assessing the consequences. Conservation Ecology **5**:8.
Kleijn, D. and I. Raemakers. 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. Ecology **89**:1811-1823.
Kleijn, D. and F. van Langevelde. 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic and Applied Ecology **7**:201-214.
Klein, A.-M., I. Steffan-Dewenter, and T. Tscharntke. 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. Proceedings of the Royal Society London Series B **270**:955-961.
Klein, A.-M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society Biological Sciences Series B **274**:303-313.
Klotz, S., I. Kühn, and W. Durka. 2002. Biolflor: eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Bundesamt für Naturschutz, Bonn.
Knight, T. M. 2003. Floral density, pollen limitation, and reproductive success in *Trillium grandiflorrum*. Oecologia **442**:557-563.
Knop, E. V. A., D. Kleijn, F. Herzog, and B. Schmid. 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. Journal of Applied Ecology **43**:120-127.
Koh, L. P., N. S. Sodhi, and B. W. Brook. 2004a. Co-extinctions of tropical butterflies and their hostplants. Biotropica **36**:272-274.
Koh, L. P., N. S. Sodhi, and B. W. Brook. 2004b. Ecological correlates of extinction proneness in tropical butterflies. Conservation Biology **18**:1571-1578.
Kolb, A. 2008. Habitat fragmentation reduces plant fitness by disturbing pollination and modifying responses to herbivory. Biological conservation **141**:2540-2549.
Kotiaho, J. S., V. Kaitala, A. Komonen, and J. Päivinen. 2005. Predicting the risk of extinction from shared ecological characteristics. Proceedings of the National Academy of Sciences of the United States of America **102**:1963-1967.

Kotze, D. J. and R. B. O´Hara. 2003. Species decline-but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. Oecologia **135**:138-148.

Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, J. Pöyry, K. M. Raatikainen, A. Sang, C. Stefanescu, T. Teder, M. Zobel5 and, and I. Steffan-Dewenter. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology Letters **13**:597-605.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2004. Landscape occupancy and local population size depends on host plant distribution in the butterfly *Cupido minimus*. Biological conservation **120**:355-361.

Kremen, C. and R. Chaplin-Kramer, editors. 2007. Insects as providers of ecosystem services: crop pollination and pest control. Royal Entomological Society of London, London.

Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences of the United States of America **99**:16812-16816.

Kruess, A. and T. Tscharntke. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. Biological conservation **106**:293-302.

Kunin, W. E. 1992. Density and reproductive success in wild populations of *Diplotaxis ercoides* (Brassicaceae). Oecologia **91**:129-133.

Kunin, W. E. 1997. Population size and density effects in pollination: pollinator foraging an plant reproductive success in experimental arrays of *Brassica kaber*. Journal of Ecology **85**:225-234.

Kwaiser, K. S. and S. D. Hendrix. 2007. Diversity and abundance of bees (Hymenoptera: Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes. Agriculture, Ecosystems and Environment **124**:200-204.

Laliberte, E., J. A. Wells, F. DeClerck, D. J. Metcalfe, C. P. Catterall, C. Queiroz, I. Aubin, S. P. Bonser, Y. Ding, J. M. Fraterrigo, S. McNamara, J. W. Morgan, D. Sanchez Merlos, P. A. Vesk, and M. M. Mayfield. 2013. Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecology Letters **13**:76-86.

Lanza, J., M. D. Warriner, and M. McHenry. 1997. Nectar derived amino acids contribute to butterfly reproduction. Bulletin of the Ecological Society of America **78**:273.

Larkin, L. L., J. L. Neff, and B. B. Simpson. 2008. The evolution of a pollen diet: host choice and diet breath of *Andrena* bees (Hymenoptera: Andrenidae). Apidologie **39**:133-145.

Le Féon, V., A. Schermann-Lgionnett, Y. Delettre, S. Aviron, R. Billeter, R. Bugter, F. Hendrickx, and F. Burel. 2010. Intensification of agriculture, landscape composition and wild bee communities: A large scale study from European countries. Agriculture, Ecosystems and Environment **137**:143-150.

León-Cortés, J. L., J. J. Lennon, and C. D. Thomas. 2003. Ecological dynamics of extinct species in empty habitat networks. 2. The role of host plant dynamics. Oikos **102**:465-477.

Leonhardt, S., K. Dworschak, T. Eltz, and N. Blüthgen. 2007. Foraging loads of stingless bees and utilisation of stored nectar for pollen harvesting. Apidologie **38**:125-135.

Lonsdorf, E., C. Kremen, T. Ricketts, R. Winfree, N. M. Williams, and S. Greenleaf. 2009. Modelling pollination services across agricultural landscapes. Annals of Botany **103**:1589-1600.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science **294**:804-808.

Lunau, K. 2004. Adaptive radiation and coevolution - pollination biology case studies. Organisms, Diversity & Evolution **4**:207-224.
Maskell, L. C., S. M. Smart, J. M. Bullock, K. E. N. Thompson, and C. J. Stevens. 2010. Nitrogen deposition causes widespread loss of species richness in British habitats. Global Change Biology **16**:671-679.
Mayer, C. 2004. Pollination services under different grazing intensities. International Journal of Tropical Insect Science **24**:95-103.
McCann, K. S. 2000. The diversity–stability debate. Nature **405**:228-233.
McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics **28**:495-516.
Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant-pollinator interactions. Ecology Letters **10**:710-717.
Memmott, J., N. M. Waser, and M. V. Price. 2004. Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society London Series B **271**:2605-2611.
Mevi-Schutz, J. and A. Erhardt. 2005. Amino acids in nectar enhance butterfly fecundity: a long-awaited link. The American Naturalist **165**:411-419.
Michener, C. D. 1954. Records and describtions of North American megachilid bees. Journal of the Kansas Entomological Society **27**:65-78.
Michez, D., S. Patiny, P. Rasmont, K. Timmermann, and N. J. Vereecken. 2008. Phylogeny and host-plant evolution in Melittidae *s.l.*(Hymenoptera: Apoidea). Apidologie **39**:146-162.
Minckley, R. L. and T. H. Roulston. 2006. Incidental mutualisms and pollen specialization among bees. Pages 69-98 *in* N. M. Waser and J. Ollerton, editors. Plant-pollinator interactions from specialization to generalization. University of Chicago Press, Chicago, Illinois, USA.
Montoya, J. M., S. L. Pimm, and R. V. Solé. 2006. Ecological networks and their fragility. Nature **442**:259-264.
Morris, M. G. 1981. Responses of grassland invertebrates to management by cutting. III. Adverse effects on Auchenorrhyncha. Journal of Applied Ecology **18**:107-123.
Morris, M. G. 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biological conservation **95**:129-142.
Morse, R. A. and N. W. Calderone. 2000. The value of honey bees as pollinators of U.S. crops in 2000. Bee Culture **128**:1-15.
Mountford, J. O., K. H. Lakhani, and F. W. Kirkham. 1993. Experimental assessment of the effects of nitrogen addition under hay-cutting. Journal of Applied Ecology **30**:321-332.
Muchhala, N., Z. Brown, W. S. Armbruster, and M. D. Potts. 2010. Competition drives specialization in pollination systems through costs to male fitness. The American Naturalist **176**:732-743.
Müller, A. 2006. Unusual host plant of *Hoplitis pici*, a bee with hooked bristles on its mouthparts (Hymenoptera: Megachilidae: Osmiini). European Journal of Entomology **103**:497-500.
Müller, A. and N. Bansac. 2004. A specialized pollen-harvesting device in western palearctic bees of the genus *Megachile* (Hymenoptera, Apoidea, Megachilidae). Apidologie **35**:329-337.
Müller, A., S. Diener, S. Schnyder, K. Stutz, C. Sedivy, and S. Dorn. 2006. Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee-flower relationships. Biological conservation **130**:604-615.
Müller, A., A. Krebs, and F. Amiet. 1997. Bienen - Mitteleuropäische Gattungen, Lebensweise, Beobachtung. Naturbuch Verlag, Augsburg.

Müller, A. and M. Kuhlmann. 2008. Pollen hosts of western palearctic bees of the genus *Colletes* (Hymenoptera:Colletidae): the Asteraceae paradox. Biological Journal of the Linnean Society **95**:719-733.

Nabhan, G. P. and S. L. Buchmann. 1997. Services provided by pollinators.*in* G. C. Daily, editor. Nature's Services: Societal dependence on natural ecosystems. Island Press, Washington, D.C.

Naeem, S. and S. Li. 1997. Biodiversity enhances ecosystem reliability. Nature **390**:507-509.

Nation, J. L. 2002. Insect physiology and biochemistry. CRC Press, Boca Raton, Florida.

Oksanen, J. 2010. Multivariate analysis of ecological communities in R: Vegan tutorial.

Oksanen, J., R. Kindt, B. Legendre, B. O´Hara, G. L. Simpson, and M. H. Stevens. 2008. Vegan: Community ecology package. R package version 1.13-2.

Olesen, J. M., J. Bascompte, H. Elberling, and P. Jordano. 2008. Temporal dynamics in a pollination network. Ecology **89**:1573-1582.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos **120**:321-326.

Owens, I. P. F. and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Science **97**:12144-12148.

Pauw, A. 2007. Collapse of a pollination web in small conservation areas. Ecology **88**:1759-1769.

Pocock, M. J. O., D. M. Evans, and J. Memmott. 2012. The robustness and restoration of a network of ecological networks. Science **335**:973-977.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomology **30**:78-85.

Praz, C. J., A. Müller, and S. Dorn. 2008. Specialized bees fail to develop on non-host pollen: Do plants chemically protect their pollen? Ecology **89**:795-804.

Proulx, M. and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology **79**:2581-2592.

Quezada-Euan, J. J. G., A. Lopez-Velasco, J. Perez-Balam, H. Moo-Valle, A. Velazquez-Madrazo, and R. J. Paxton. 2011. Body size differs in workers produced across time and is associated with variation in the quantity and composition of larval food in *Nannotrigona perilampoides* (Hymenoptera, Meliponini). Insectes Sociaux **58**:31-38.

Rabie, A. L., J. D. Wells, and L. K. Dent. 1983. The nitrogen content of pollen protein. Journal of Apicultural Research **22**:119-123.

Rands, M. R. W., W. M. Adams, L. Bennun, S. Butchart, A. Clements, D. Coomes, A. Entwistle, I. Hodge, V. Kapos, J. Scharlemann, W. Sutherland, and B. Vira. 2010. Biodiversity conservation: Challenges beyound 2010. Science **329**:1298-1303.

Rathcke, B. J. and E. S. Jules. 1993. Habitat fragmentation and plant pollinator interactions. Current Science (Bangalore) **65**:273-277.

Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmanek. 2000. Plant invasions - the role of mutualism. Biological Review **75**:65-93.

Robinson, G., S. Willard, R. Nowogrodski, and R. A. Morse. 1989. The value of honey bees as pollinators of US crops. American Bee Journal **129**:477-487.

Rook, A. J., B. Dumont, J. Isselstein, K. Osoro, M. F. WallisDeVries, G. Parente, and J. Mills. 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. Biological conservation **119**:137-150.

Roubik, D. W. 1978. Competitive interactions between neotropical pollinators and africanized honey bees. Science **201**:1030-1032.

Roulston, T. H. and S. L. Buchmann. 2000. A phylogenetic reconsideration of the pollen starch-pollination correlation. Evolutionary Ecology Research **2**:627-643.

Roulston, T. H. and J. H. Cane. 2000. Pollen nutritional content and digestibility for animals. Plant Systematics and Evolution **222**:187-209.

Roulston, T. H. and J. H. Cane. 2002. The effect of pollen protein concentration on body size in the sweat bee *Lasioglossum zephyrum* (Hymenoptera: Apiformes). Evolutionary Ecology **16**:49-65.

Roulston, T. H., J. H. Cane, and S. L. Buchmann. 2000. What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny? Ecological Monographs **70**:617-643.

Schaffers, A. P., I. P. Raemakers, K. V. Sýkora, and C. J. F. ter Braak. 2008. Arthropod assemblages are best predictedby plant species composition. Ecology **89**:782-794.

Schemske, D. W. and C. C. Horvitz. 1984. Variation among floral visitors in pollination ability: A precondition for mutualism specialization. Science **225**:519-521.

Scheper, J., M. Reemer, R. van Kats, W. A. Ozinga, G. T. J. van der Linden, J. H. J. Schaminée, H. Siepel, and D. Kleijn. 2014. Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. Proceedings of the National Academy of Sciences **111**:17552-17557.

Schweiger, O., J. C. Biesmeijer, R. Bommarco, T. Hickler, P. Hulme, S. Klotz, I. Kühn, M. Moora, A. Nielsen, R. Ohlemüller, T. Petanidou, S. G. Potts, P. Pysek, J. C. Stout, M. Sykes, T. Tscheulin, M. Vila, G.-R. Walther, C. Westphal, M. Winter, M. Zobel, and J. Settele. 2010. Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. Biological Reviews **85**:777-795.

Schweiger, O., J. Settele, O. Kudrna, S. Klotz, and I. Kühn. 2008. Climate change can cause spatial mismatch of trophically interacting species. Ecology **89**:3472-3479.

Sedivy, C., C. J. Praz, A. Müller, A. Widmer, and S. Dorn. 2008. Patterns of host-plant choice in bees of the genus *Chelostoma*: the constraint hypothesis of host-range evolution in bees. Evolution **62**:2487-2507.

Silander, J. A. 1978. Density-dependent control of reproductive success in *Cassia biflora*. Biotropica **10**:292-296.

Simons, N. K., W. W. Weisser, and M. M. Gossner. 2015. Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient. Ecology:DOI: 10.1890/1815-0616.1891.

Sjödin, N. E., J. Bengtsson, and B. Ekbom. 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. . Journal of Applied Ecology **45**:763-772.

Socher, S. A., D. Prati, S. Boch, J. Müller, H. Baumbach, S. Gockel, A. Hemp, I. Schöning, K. Wells, F. Buscot, E. K. V. Kalko, K. E. Linsenmair, E.-D. Schulze, W. W. Weisser, and M. Fischer. 2013. Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. Basic and Applied Ecology **14**:126-136.

Socher, S. A., D. Prati, S. Boch, J. Müller, V. H. Klaus, N. Hölzel, and M. Fischer. 2012. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. Journal of Ecology **100**:1391-1399.

Southwick, E. E. and L. Southwick. 1992. Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. Economic Entomology **85**:621-633.

Spigler, R. B. and S.-M. Chang. 2009. Pollen limitation and reproduction varies with population size in experimental populations of *Sabatia angularis* (Gentianaceae). Botany **87**:330-338.

Spira, T. 2001. Plant-pollinator interactions: A threatened mutualism with implications for the ecology and management of rare plants. Natural Areas Journal **21**:78-88.

Standifer, L. N. 1967. A comparison of the protein quality of pollens for growth stimulation and hypopharyngeal glands and longevity of honey bees (*Apis mellifera*, Hymenoptera, Apidae). Insectes Sociaux **14**:415-426.

Steffan-Dewenter, I. 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Biological conservation **17**:1036-1044.

Steffan-Dewenter, I., S. G. Potts, and L. Packer. 2005. Pollinator diversity and crop pollination services are at risk. Trends in Ecology and Evolution **20**:652-653.

Steffan-Dewenter, I. and T. Tscharntke. 2001. Succession of bee communities on fallows. Ecology **24**:83-93.

Strauss, S. Y. and A. R. Zangerl. 2002. Plant-insect interactions in terrestrial ecosystems. Pages 77-106 *in* C. M. Herrera and O. Pellmyr, editors. Plant-animal interactions - an evolutionary approach. Blackwell Publishing, Malden.

Strickler, K. 1979. Specialization and foraging efficiency of solitary bees *Hoplitis anthocopoides*. Ecology **60**:998-1009.

Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Science **102**:4387-4392

Tasei, J.-N. l. and P. Aupinel. 2008. Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (Bombus terrestris, Hymenoptera: Apidae). Apidologie **39**:397-409.

Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings of the Royal Society of London. Series B: Biological Sciences **268**:1791-1796.

Thorp, R. W. 1969. Systematics and ecology of bees of the subgenus *Diandrena* (Hymenoptera: Andrenidae). University of California Publications in Entomology **52**:1-146.

Thorp, R. W. 2000. The collection of pollen by bees. Plant Systematics & Evolution **222**:211-223.

Tilman, D., C. Balzer, J. Hill, and B. L. Befort. 2011. Global food demand and the sustainable intensification of agriculture. Proceedings of the National Academy of Science **108**:20260-20264.

Tilman, D. and J. A. Downing. 1994. Biodiversity and stability in grasslands. Nature **367**:363-365.

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science **277**:1300-1302.

Tudor, O., R. L. H. Dennis, J. N. Greatorex-Davies, and T. H. Sparks. 2004. Flower preferences of woodland butterflies in the UK: Nectaring specialists are species of conservation concern. Biological conservation **119**:397-403.

Tylianakis, J. M., T. Tscharntke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. Nature **445**:202-205.

Vamosi, J., T. M. Knight, J. A. Steets, S. J. Mazer, M. Burd, and T. L. Ashmann. 2006. Pollination decays in biodiversity hotspots. Proceedings of the National Academy of Science **103**:956-961.

van Swaay, C. A. M. 2002. The importance of calcareous grasslands for butterflies in Europe. Biological conservation **104**:315-318.

Vaughton, G. and M. Ramsey. 1998. Floral display, pollinator visitation and reproductive success in the dioecious perennial herb *Wurmbea dioica* (Liliaceae). Oecologia **115**:93-101.

Vázquez, D. P. 2005. Degree distribution in plant-animal mutualistic networks: forbidden links or random interactions? Oikos **108**:421-426.

Vázquez, D. P. and M. A. Aizen. 2003. Null model analyzes of specialization in plant-pollinator interactions. Ecology **84**:2493-2501.

Vázquez, D. P. and M. A. Aizen. 2006. Community-wide patterns of specialization in plant-pollinator interactions revealed by null modles. Pages 200-219 *in* N. M. Waser and J. Ollerton, editors. Plant-pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago.

Vázquez, D. P., N. Chacoff, and L. Cagnolo. 2009. Evaluating multiple determinants of the structure of mutualistic networks: comment. Ecology **90**:2039-2046.

Vázquez, D. P. and D. Simberloff. 2002. Ecological specialization and susceptibility to disturbance: conjectures and refutations. American Naturalist **159**:606-623.

Wäckers, F. L. 1999. Gustatory response by the hymenopteran parasitoid *Cotesia glomerata* to a range of nectar and honeydew sugars. Journal of Chemical Ecology **25**:2863-2877.

Waites, A. R. and J. Agren. 2004. Pollinator visitation, stigmatic pollen loads and among-population variation in seed set in *Lythrum salicaria*. Journal of Ecology **92**:512-526.

Waser, N. M. 2006. Specialization and generalization in plant-pollinator interactions: a historical perspective. Pages 3-17 *in* N. M. Waser and J. Ollerton, editors. Plant-pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago.

Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. Ecology **77**:1043-1060.

Waser, N. M. and J. Ollerton, editors. 2006. Plant-pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago.

Weiner, C., M. Werner, K. E. Linsenmair, and N. Blüthgen. 2011. Land-use intensity in grasslands: changes in biodiversity, species composition and specialization in flower-visitor networks. Basic and Applied Ecology **12**:292-299.

Weiner, C. N., M. Werner, K. E. Linsenmair, and N. Blüthgen. 2014. Land-use impacts on plant–pollinator networks: interaction strength and specialization predict pollinator declines. Ecology **95**:466-474.

Westrich, P. 1990. Die Wildbienen Baden-Württembergs II. Eugen Ulmer Verlag, Hohenheim.

Wille, H., M. Wille, V. Kilchenmann, A. Imdorf, and G. Bühlmann. 1985. Pollenernte und Massenwechsel von drei *Apis mellifera*-Völkern auf demselben Bienenstand in zwei aufeinanderfolgenden Jahren. Revue Suisse de Zoologie **92**:897-914.

Williams, N. M. 2003. Use of novel pollen species by specialist and generalist solitary bees (Hymenoptera: Megachilidae). Oecologia **134**:228-237.

Winfree, R., T. Griswold, and C. Kremen. 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology **21**:213-223.

Wisskirchen, R. and H. Haeupler. 1998. Standardliste der Farn- und Blütenpflanzen Deutschlands. Verlag Eugen Ulmer, Stuttgart.

Yachi, S. and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Science **96**:1463-1468.

Zechmeister, H. G., I. Schmitzberger, B. Steurer, J. Peterseil, and T. Wrbka. 2003. The influence of land-use practices and economics on plant species richness in meadows. Biological conservation **114**:165-177.

Acknowlegements

I want to express my sincere gratitude to **Nico Blüthgen.** I thank you for your patience with all my questions, ideas and moods, for always finding the time for discussion, for our walks around university whenever they where needed and for being such a great advisor and listener no matter what was going on. Without your constant critic and support throughout the thesis and your motivation work this PhD project would not have been possible. You were a great supervisor to learn from.

I furthermore thank **Karl-Eduard Linsenmair**, my co-supervisor during the first years of my PhD, for his interest, his encouragement and kindness, constructive criticism and contribution of many fruitful ideas and **Andreas Jürgens** for his agreement on taking over the co-supervision of my PhD thesis when I switched to TU Darmstadt.

Almost countless people helped me to manage working on this challenging project. For identification of insects, I would like to thank **Wolfgang Adaschkiewitz**, **Rainer Heiß**, **Gisela Merkel-Wallner**, **Bernhard Merz**, **Verner Michelsen**, **Sabine Prescher**, **Hans-Georg Rudzinski**, **Andreas Stark**, **Krzysztof Szpila**, **Martina Tospann**, **Michael von Tschirnhaus**, **Hans-Peter Tschorsnig** (Diptera); **Dieter Doczkal** (Apidae, Syrphidae); **Martin Fellendorf**, **Mike Hermann**, **Volker Mauss**, **Hans Schwenninger** (Apidae); **Klaus Horstmann**, **Seraina Klopfstein** (Ichneumonidae), **Lasse Hubweber**, **Peter Sprick** (Coleoptera); **Manfred Krauss**, **Beate Wende** (Symphyta); **Roland Schultz** (Formicidae) and **Mirko Wölfling** (Lepidoptera).

For field work permits my thanks go to the responsible **state environmental offices of Baden-Württemberg**, **Thüringen**, **and Brandenburg** (according to § 72 BbgNatSchG). The work has been funded by the **DFG Priority Program** 1374 "Infrastructure-Biodiversity-Exploratories" (LI 150/20-1).

Anna Hellwig, **Mathias Hoffmeister, Matthias Jäger**, **Susann Janowski**, **Linda Jung**, **Daniel Schaub, Martina Tospann, Beate Wende** and **Michael Werner** all had their part gaining data on plant-pollinator interactions during the field season. Their help was indispensable. **Andrea Hilpert** spent endless hours with collecting, preparing and analysing pollen samples and was one of the most important persons behind the scenes as well as **Dorothea Hahne** and **Verena Seufert** who patiently assisted with pollen collection in the laboratory.

I further like to thank the entire team of the Biodiversity Exploratories for their logistic support. My special thanks go to **Simone Pfeiffer** who beneath being a fabulous project

coordinator, manages to be a great listener, advisor and motivator for so many people and does an amazing job for the community. **Jens Nieschulze** encouraged me to use R (which proved to be an invaluable facilitation after some challenging time), helped me when I was frustrated by the program, always managed to give me the feeling I would finally succeed and together with **Carsten Dormann** was a marvellous advisor in programming R.

Michael Werner was the one to teach me all the plant species in the beginning, had a never ending patience with me forgetting their names, was a great field mate and the one to discuss the details of the project.

Martina Tospann became the one to make me laugh or calm me down whenever things went wrong. Her tranquillity and encouragement are just indescribable. She is a perfect lab and field mate and became a really good friend.

Mareike Hillerkus, **Yvonne Heyde**, **Axel** and **Alicia Kirste, Tim Haarmann** and **Ingo Misgeld** are the ones who since many years are invaluable companions in the jungle of life, who have always been the foothold I could count on and whose friendship makes earth a place worth living.

Rolf Schulte somehow managed to motivate me to continue and finally finish my PhD thesis. He is the foothold I can count on.

Last but not least I want to thank my parents, **Barbara** and **Rudolf Weiner** who always gave their best to offer me all the opportunities I could have longed for, who patiently waited when their farsick daughter was exploring the world, who just were there when I once again made my own experiences and who gave me their unconditional love, friendship and support. There is no place like home.

Curriculum Vitae

Dipl. Biol. Christiane Weiner

Siebenkluster 3
27711 Osterholz-Scharmbeck
e-mail:christiane.weiner@gmx.de

Education

12/2012 – 04/2016	PhD in biology, Technische Universität Darmstadt, Germany PhD thesis: 'Diversity and resource choice of flower visiting insects in relation to pollen nutritional quality and land use'. Supervised by Prof. Dr. N. Blüthgen
02/2007 – 06/2010	Julius-Maximilians-University, Würzburg, Department of Animal Ecology and Tropical Biology. PhD studies. Supervised by Prof. Dr. N. Blüthgen and Prof. Dr. K.-E. Linsenmair
05/2006	Diploma in biology; grade point average: 1.0 (A)
09/2005 – 05/2006	Diploma thesis at the University of Bremen, Germany 'Limiting factors for the short-term recruitment of savanna trees at woodland islands in the Western Soutpansberg, South Africa' *Field trip to Limpopo Province, Republic of South Africa* *Scholarship of the German Academic Exchange Service (DAAD)*
10/2001 – 08/2005	Study of Biology at the University of Bremen, Germany
08/1992 – 06/2001	College student, St. Joseph Gymnasium, Rheinbach, Germany University entrance exam (Abitur), grade point average: 1.9

Voluntary work

02/2005 - 04/2005	Internship with the Black Vulture Conservation Foundation (BVCF), Spain
06/2002 – 08/2002	Internship at the Zoological Garden Wroclaw, Poland

Teaching and Supervision

02/2007 – 06/2010	University of Würzburg, Germany Co-supervision of two diploma theses Supervision of field work projects and excursions Supervision of a course on insect determination

04/2003– 07/2005	University of Bremen, Germany Supervision of several courses on insect determination, plant physiology, plant determination and animal physiology

Work experience

Since 03/2014	Research associate at Avitec Research GbR in Osterholz-Scharmbeck
09/2013 - 02/2014	Secondary school teacher at the Tomburg Realschule in Rheinbach *Subjects: biology and chemistry*
07/2013 - 10/2013	Freelancer for GrünWerk and Eich Landschaftsplanerische Leistungen
01/2013 - 03/2013	Assistant in a short-term project at Stiftung Rheinische Kulturlandschaft
08/2010 - 08/2012	Secondary school teacher at the Maria-Sibylla-Merian Gymnasium in Krefeld *Subjects: biology, politics, chemistry and physics*
09/2011 – 07/2012	Secondary school teacher at Fichte Gymnasium Krefeld *Subject: geography*
02/2007 – 06/2010	PhD student at Julius-Maximilians-University, Würzburg, Department of Animal Ecology and Tropical Biology
09/2006 – 02/2007	Employee at the Black Vulture Conservation Foundation, (BVCF) Spain
06/2006 – 08/2006	Assistant researcher at the University of Bremen, Department of Vegetation Ecology

Languages

Mother tongue	German
Second languages	English (fluent) Polish (fluent) Spanish (modest) Latin

Interests

Hiking	Poetry	Literature
Travelling	Photography	Nature conservation

Author contributions

Chapter 3 has been published as:
Weiner, C.N., Werner, M., Linsenmair, K.-E., Blüthgen, N. (2011): Land-use intensity in grasslands: changes in biodiversity, species composition and specialization in flower-visitor networks. Basic and Applied Ecology 12 (4), 292-299.

CNW, MW and NB designed the study, NB and KEL conceived the project, CNW and MW performed the fieldwork. CNW performed the statistical analysis and drafted the first version of the manuscript, CNW, KEL and NB contributed to writing.

Chapter 4 has been published as:
Weiner, C.N., Werner, M., Linsenmair, K.-E., Blüthgen, N.: Land-use impacts on plant–pollinator networks: interaction strength and specialization predict pollinator declines. Ecology 95:466–474.

CNW and NB are the principal authors and drafted the manuscript, KEL contributed to writing. KEL and NB conceived the project, CNW performed the statistical analysis, CNW and MW performed the fieldwork.

Chapter 5 will be submitted as:
Weiner, C., Werner, M., Blüthgen, N. (in prep): Land-use intensification triggers diversity loss in pollination networks: Regional distictions between three different German bioregions

CNW and NB designed the study, NB conceived the project, CNW and MW performed the fieldwork. CNW performed the statistical analysis and wrote the manuscript.

Chapter 6 has been published as:
Weiner, C.N., Hilpert, A., Werner, M., Linsenmair, K.-E., Blüthgen, N. (2010): Pollen amino acids and flower specialization in solitary bees. Apidologie 41 (4), 476-487.

CNW, NB and KEL designed the study, CNW and AH collected the pollen samples, AH and CNW performed the pollen analysis, CNW performed the statistical analysis and wrote the first version of the manuscript, MW, NB and KEL commented on the manuscript.

List of publications

Gamez-Virues S, Perovic D, Gossner MM, Börschig C, Blüthgen N, de Jong H, Simons NK, Klein AM, Krauss J, Maier G, Scherber C, Steckel J, Rothenwöhrer C, Steffan-Dewenter I, Weiner CN, Weisser W, Werner M, Tscharntke T & Westphal C (2015) *Landscape simplification filters species traits and drives biotic homogenization.* **Nat. Commun**. 6:8568.

Allan E, Manning P, Alt F, Binkenstein J, Blaser S, Blüthgen N, Böhm S, Grassein F, Hölzel N, Klaus VH, Kleinebecker T, Morris EK, Oelmann Y, Prati D, Renner SC, Rillig MC, Schaefer M, Schloter M, Schmitt B, Schöning I, Schrumpf M, Solly E, Sorkau E, Steckel J, Steffen-Dewenter I, Stempfhuber B, Tschapka M, Weiner CN, Weisser WW, Werner M, Westphal C, Wilcke W Fischer M (2015) *Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition.* **Ecology Letters** 18: 834–843.

Manning P, Gossner MM., Bossdorf O, Allan E, Zhang YY, Prati D, Blüthgen N, Boch S, Böhm S, Börschig, C., Hölzel, N., Jung, K., Klaus, V. H., Klein, A. M., Kleinebecker T, Krauss J, Lange M, Müller J, Pašalić E, Socher SA, Tschapka M, Türke M, Weiner, C., Werner M, Gockel S, Hemp A, Renner SC, Wells K, Buscot F, Kalko EKV, Linsenmair KE, Weisser WW and Fischer M (2015) *Grassland management intensification weakens the associations among the diversities of multiple plant and animal taxa.* **Ecology** 96: 1492–1501.

Renoult JP, Blüthgen N, Binkenstein J, Weiner CN, Werner M, Schaefer HM (2014) *The relative importance of color signaling for plant generalization in pollination network.* **Oikos** DOI: 10.1111/oik.01361

Weiner CN, Werner M, Linsenmair KE, Blüthgen N (2014) *Land-use impacts on plant–pollinator networks: interaction strength and specialization predict pollinator declines.* **Ecology** 95:466–474.

Allan E, Bossdorf O, Dormann CF, Prati D, Gossner MM, Tscharntke T, Blüthgen N, Bellach M, Birkhofer K, Boch S, Böhm S, Börschig C, Chatzinotas A, Christ S, Daniel R, Diekötter T, Fischer C, Friedl T, Glaser K, Hallmann C, Hodac L, Hölzel N, Jung K, Klein AM, Klaus VH, Kleinebecker T, Krauss J, Lange M, Morris MK, Müller J, Nacke H, Pašalić E, Rillig MC, Rothenwöhrer C, Schall P, Scherber C, Schulze W, Socher SA, Steckel J, Steffan-Dewenter I, Türke M, Weiner CN, Werner M, Westphal C, Wolters V, Wubet T, Gockel S, Gorke M, Hemp A, Renner SC, Schöning I, Pfeiffer S, König-Ries B, Buscot F, Linsenmair KE, Schulze ED, Weisser WW, Fischer M (2014*) Interannual variation in land-use intensity enhances grassland multidiversity.* **PNAS** 111: 308-313.

Chrobock T, Weiner CN, Werner M, Blüthgen N, Fischer M, van Kleunen M (2013) *Effects of native pollinator specialization, self-compatibility and flowering duration of European plant species on their invasiveness elsewhere.* **Journal of Ecology** 101(4): 916–923

Schleuning M, Fründ J, Klein AM, Abrahamczyk S, Alarcón R, Albrecht M, Andersson GKS, Bazarian S, Böhning-Gaese K, Bommarco R, Dalsgaard B, Dehling M, Gotlieb A, Hagen M, Hickler T, Holzschuh A, Kaiser-Bunbury C, Kreft H, Morris RJ, Sandel B, Sutherland WJ, Svenning JC, Tscharntke T, Watts S, Weiner CN, Werner M, Williams NM, Winqvist C, Dormann CF, Blüthgen N (2012) *Specialization of Mutualistic Interaction Networks Decreases toward Tropical Latitude,* **Current Biology** 22 (20): 1925–1931

Blüthgen N, Dormann C, Alt F, Boch S, Klaus V, Kleinebecker T, Gockel S, Nieschulze J, Renner S, Schumacher U, Birkhofer K, Buscot F, Fischer M, Hemp A, Hölzel N, Kalko EKV, Linsenmair KE, Oelmann Y, Prati D, Rothenwöhrer C, Scherber C, Schöning I, Schulze E.-D., Tscharntke T, Weiner CN, Wells K, Weisser WW (2012). A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. **Basic and Applied Ecology** 13 (3), 207-220.

Weiner CN, Werner M, Linsenmair KE, Blüthgen N (2011) *Land-use intensity in grasslands: changes in biodiversity, species composition and specialisation in plant - flower visitor networks.* **Basic and Applied Ecology** 12 (4), 292-299.

Weiner CN, Hilpert A, Werner M, Linsenmair KE, Blüthgen N (2010) *Pollen amino acids and flower specialisation in solitary bees.* **Apidologie** 41 (4), 476-487.

Conference contributions (selection)

Weiner CN, Werner M, Linsenmair KE, Blüthgen N (2012) Monitoring von Blütenbesuchernetzwerken entlang von Landnutzungsgradienten im Grünland. Nationales Biodiversitätsmonitoring 2020, NeFo Workshop 14.-15. Juni, Berlin

Weiner CN, Werner M, Linsenmair KE, Blüthgen N (2010) Intensive land use triggers losses in flower diversity and specialised pollinators. EcoFlor 2010, La Laguna, Tenerife, Spain

Weiner CN, Werner M, Linsenmair KE, Blüthgen N (2009) Land-use intensity in grasslands: Changes in biodiversity, species composition and specialisation in flower-visitor networks. 23rd SCAPE meeting [Scandinavian Association for Pollination Ecologists], Seili, Finnland

Weiner CN, Werner M, Linsenmair KE, Blüthgen N (2008) Do bees suffer from land-use intensification? Jahrestagung der Gesellschaft für Ökologie (GfÖ), Leipzig

Weiner CN, Werner M, Hilpert A, Linsenmair KE, Blüthgen N (2007) Pollen amino acids, plant taxonomy and specialisation in solitary bees. 21st SCAPE meeting [Scandinavian Association for Pollination Ecologists], Århus, Denmark